

COMPETITION FOR ABOVE AND BELOW GROUND RESOURCES AMONG
ANNUAL SPECIES FROM THE PLANT TO THE FIELD: QUANTIFICATION
ANALYSIS AND MODELING

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The ability to compete for resources is a main determinant of a plant's success within a plant community. In the case of agricultural crops, competition among weeds and crop plants is a major determinant of crop yield losses. The objectives of this study are: i) to improve the understanding of the role of weeds in water use and crop water productivity, ii) to test, through field experiments and an individual based model, the effects of size inequality and plant spatial arrangements on the competitive relationships among plants, the success of individuals, the evolution of plant sizes distributions and the ability of individual plants to capture resources, and iii) to explore through a modeling exercise the effects of soil nitrogen and weather on competitive growth of *Abutilon theophrasti* M. (velvetleaf) and *Zea mays* L. (maize). For this purpose a mechanistic individual based model was developed, which estimates light interception, photosynthesis, respiration, growth, photosynthate allocation and root growth at the leaf or plant level, allowing plants to compete for solar radiation and soil resources. Each of the model components had been calibrated and cross validated with data collected on field experiments where maize and maize-*A.theophrasti* mixtures were established on 2005, 2006 and 2007 with *A. theophrasti* plants emerging before, simultaneously and after maize. In these experiments

intensive measurements of plant height, plant leaf area, leaf area distribution, plant biomass, leaf stomatal conductance, soil water extraction and yield were taken, providing additional experimental evidence to this research. Despite exceptionally dry conditions in the field in some years, maize-weed mixtures and maize in monocrop had similar total soil water contents and rates of water extraction through the profile and maize was no more water stressed in the weedy treatments than in monocrop. However the partitioning of transpired water among plant species shifted according to the amount of leaf area and height of the plants, which ultimately determined the amount of solar radiation intercepted. Plant size distributions for each species cohort changed over time, becoming more positively skewed as the dominant plants in the cohort capitalized on their advantage. This effect was more obvious as competition for resources was intensified by greater availability of water and nitrogen or when the species cohort became dominated by another cohort of plants (i.e. due to timing of emergence or spatial arrangement of rows). High soil nitrogen availability enhanced maize competitiveness, suppressing weeds and reducing yield loss, especially when other environmental factors allowed high maize yield potentials. High soil nitrogen levels and in season weather also changed the relative heights of maize and weeds (height difference), which were closely related to maize yield loss and therefore were good early predictors of maize yield loss. Weather effects on yield loss were guided primarily by changes on soil nitrogen availability and changes in the rates plant growth that modified both nitrogen uptake and the dynamics of competition for other resources. Both model and field results also highlight that maize-*A. theophrasti* competition is highly dynamic, and dependent on the initial conditions, primarily plant sizes and rates of growth. The analysis of how crop and weeds compete for resources can not only help reduce crop yield losses due to weeds, but also contribute to understanding how plant communities in natural systems respond to the environment.

BIOGRAPHICAL SKETCH

Andrés G. Berger was born April 24, 1976. He grew up in Colonia Valdense in the state of Colonia in the south west of Uruguay. He graduated from Liceo Daniel Armand Ugón in 1993 after which he moved to Montevideo to pursue undergraduate studies in Agronomy in Universidad de la República, Facultad de Agronomía. After his graduation he started to work in the same institution as a research associate working on soil fertility management of rice-pasture systems. He later appointed as entry-level professor, lecturing in courses at the undergraduate program. In 2003 he was awarded a Fulbright grant and an OAS grant and started a MS program in the Field of Soil and Crop Sciences at Cornell University and after completion enrolled in a PhD program in the same field with support from the Department of Crop and Soil Sciences.

To our son Alex, a continuous source of motivation.

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CHAPTER 1

DO WEEDS EXACERBATE WATER STRESS IN MAIZE CROPS IN THE US NORTHEAST?

ABSTRACT

Water transpired by weeds could exacerbate crop drought stress in dry periods through increasing soil moisture deficits, resulting in a decrease in crop water productivity. However, weed-crop competition for water is dynamic, as water uptake depends on the relative growth of the crop vs. the weeds and plant stress status depends on the amount of solar-radiation intercepted in relation to available stored soil water. To evaluate dynamic outcomes of crop-weed competition, a simulation model was developed and additive experiments established to test the model, with maize in monoculture and in combination with high-density stands of velvetleaf (*Abutilon theophrasti* M.). Velvetleaf was planted before (EE), simultaneously (SE) and after maize (LE), generating a range of competitive scenarios from high to low. Despite exceptionally dry conditions at the field in some years, we found no evidence that the maize-weed mixtures had less total soil water or different rates of water extraction through the profile than the maize monocrop. It appears that soil water dynamics and drought severity were not significantly affected by weed competition. However the partitioning of water transpired among plant species shifted according to the amount and height distribution of each plant's leaf area, which determined the amount of solar radiation intercepted (maize transpiration was 37, 72 and 94 % of the total at EE, SE, LE respectively). The similar total water use implied that crop water productivity changes were more closely related to maize yield loss than to changes in water use. The simulations indicated that the presence of weeds is only likely to influence the soil water balance and drive the crop into stress if

a dry spell occurs within a relatively narrow period of time at the beginning of the growing season, between approximately 30-50 days after emergence.

INTRODUCTION

Common wisdom suggests that weeds compete for soil water, nutrients and light and therefore weed management is considered a key management practice in increasing crop water use efficiency and productivity. However detailed analysis of weed competition under different resource availability scenarios is missing.

Research has shown that in water-limited environments where crops experience severe or terminal droughts during the growing season, the major impacts of agronomic management practices comes from increasing the amount of water transpired by the crop through the reduction in the amount of water lost by soil evaporation or used by weeds, and not necessarily through the reduction of the total amount of evapotranspiration (Turner 2004). That is especially the case for Mediterranean type environments, where fall and winter rainfalls combined with low evaporative demand allow the growth of winter crops during the cold seasons, but low rainfall, in conjunction with high evaporative demand, is insufficient to sustain a crop during the warm season. A different, less extreme scenario is the one observed in sub-humid and humid regions during summer time, where erratic rainfalls leading to dry spells can produce water stress and considerable yield losses in some years, affecting different growth stages of the crops (Barron, Rockstrom et al. 2003). Less research effort has been deployed to study the effects of water shortages in these systems, and the recommendations on weed management with respect to competition for soil water usually come from experience gathered under water-limited environments. Given that forecasts of climate change predict increased frequency and severity of dry spells combined with extreme events of

precipitation (Tebaldi, Hayhoe et al. 2006), a detailed analysis of weed competition for water is justified.

Current weed management practices have to address the challenge of managing weeds to maintain yield losses below a predefined economic threshold while, at the same time, sustaining sufficient weed populations to take advantage of ecosystem services that they may provide (Kleijn, Baquero et al. 2006). Weed management as opposed to total weed control is consequently considered the recommended practice at the field scale (Marshall, Brown et al. 2003) as well as the landscape scale (Tscharntke, Klein et al. 2005). It is imperative therefore to have a sound understanding of the mechanisms involved in weed competition for resources in order to make informed decisions on weed management.

To understand the effects of weed competition on crop yield it is important to characterize the dynamics of growth and resource capture by the competing species, as they have been recognized as key factors in determining the final outcomes of competition (Schwinning, Weiner 1998). A large number of studies have focused on the size-symmetry/asymmetry of competition for resources, that is, if the share of the contested resource is in proportion with the size of the plant or not. For example, size-asymmetry in competition for light has been recognized by a number of researchers (Schwinning, Weiner 1998, Freckleton, Watkinson 2001) and has been linked to the formation of hierarchies in the canopy, whereby plants occupying the upper layers of the canopy capture a disproportionately large fraction of the contested resources compared to their sizes, achieve higher growth rates, and further enhance their position within the canopy. In contrast, a number of studies have shown size-symmetry (Berntson, Wayne 2000, Cahill, Casper 2000) as well as niche differentiation (Parrish, Bazzaz 1976) in the case soil resources capture. The concept of size-symmetry, though useful, can fail to recognize that competition for resources under changing environments is dynamic and that competition for one resource (e.g. light) may interfere with the ability to compete for

another resource (e.g. soil water) (Schwinning, Weiner 1998). For example, a dominant plant would intercept a large proportion of the incoming light and have the opportunity to achieve high growth rates if it is also capable of exploiting enough soil water to meet the demand and avoid becoming water stressed. Thus the ability of this dominant plant (with a size asymmetric advantage) to realize high growth rates will depend on the ability to compete for soil water as well (which is thought to be size symmetric), demonstrating the interdependence of above and below ground competition and the fragility of the size symmetry/asymmetry concept. The interdependence among limiting resources and the dynamic behavior of competition has been demonstrated in the literature by the diversity of outcomes of competition that can be observed for what are initially expected to be similar scenarios of crop-weed competition (i.e. similar weed and crop densities, emergence times, experimental locations, or soil properties) (Fischer, Harvey et al. 2004, Lindquist, Mortensen et al. 1996), and has motivated the use of ecophysiological models to better understand the processes and dynamics of competition. In this context, this study aims to gain understanding of the effects that resource availability have on crop-weed competitive relationships and the impacts of competition on resource use. The objectives of this study are: i) characterize water use patterns through the growing season and in the soil profile for a weedy crop vs. weed free crop; ii) estimate crop water productivity in the field, and analyze the factors driving it through model simulations; iii) characterize water stress status of the different species in the plant community and its relationship with light interception patterns and root growth; iv) improve the understanding of the role of weeds on water use and crop water productivity under the climatic conditions of the US Northeast.

MATERIALS AND METHODS

Site description

Field experiments were conducted at a Cornell University experimental farm located in Ithaca, NY (42°27'N, 76°27'W) during the 2005, 2006 and 2007 growing seasons (May-August). The study took place on the same field over the three years, which has a soil type dominated by well drained Williamson silt loam soil (coarse-silty, mixed, active, mesic Typic Fragiudepts), with bulk densities at 0.1, 0.3 and 0.5 m depth of 1.27 ± 0.02 , 1.47 ± 0.03 , 1.52 ± 0.02 g cm⁻³. The upper drained volumetric soil water content (estimated from moisture readings), and the permanent wilting point (estimated as soil water content at -1.5 MPa) were 0.30, 0.35, 0.37, 0.41 and 0.11, 0.21, 0.23, 0.23 at 0.1, 0.3, 0.5 and 1 m depth respectively. Daily weather was obtained from a weather station located at less than 1km from the site (Table 1.1). The 2005 growing season was characterized by wetter than normal early summer (May, June), normal (July, August) and drier than normal (September), with temperatures on average 1.3°C warmer than normal through the summer. Temperatures during the 2006 growing season were close to normal; however it was significantly wetter than normal except for May and a dry spell occurring around and after maize anthesis during mid August. Finally both temperatures and precipitation were between the normal ranges for the 2007 growing season.

Table 1.1 Monthly precipitation, temperature, and climatic normals for the experimental site. Errors are standard errors of the mean.

Month	Days	Mean air temperature				Precipitation (Reference evapotranspiration in parenthesis)			
		2005	2006	2007	30 yr. average	2005	2006	2007	30 yr. average
		°C				mm			
MAY	1-15	10 ± 1.4	13 ± 0.8	11 ± 1.4	12 ± 4.9	13 (52)	28 (51)	12 (60)	43
	16-31	11 ± 0.6	13 ± 1.4	15 ± 1.5	15 ± 4.7	22 (47)	34 (47)	12 (60)	42
JUNE	1-15	23 ± 0.9	16 ± 0.9	19 ± 1.0	17 ± 4.2	61 (65)	87 (38)	29 (60)	42
	16-30	20 ± 1.2	21 ± 0.7	20 ± 1.2	19 ± 3.8	78 (58)	104 (57)	44 (66)	51
JULY	1-15	22 ± 0.8	21 ± 0.7	19 ± 1.1	20 ± 3.5	17 (62)	106 (58)	46 (59)	44
	16-31	23 ± 0.7	23 ± 0.6	20 ± 0.7	21 ± 3.2	18 (67)	66 (64)	76 (57)	52
AUGUST	1-15	24 ± 0.5	21 ± 1.2	21 ± 0.7	20 ± 3.3	6 (63)	13 (62)	42 (56)	47
	16-31	20 ± 0.7	19 ± 0.5	19 ± 0.9	19 ± 3.5	65 (55)	110 (39)	30 (49)	47
SEPTEMBER	1-15	18 ± 0.7	16 ± 0.5	19 ± 1.0	17 ± 4.0	15 (51)	45 (30)	81 (48)	43
	16-30	16 ± 0.9	15 ± 1.0	17 ± 1.4	14 ± 4.2	39 (38)	22 (32)	7 (35)	62

The experimental design was a randomized complete block, with three replicates in 2005 and five replicates in 2006 and 2007. In each plot (plot size 4x3m), an access tube for a portable dielectric probe (PDP) (Delta-T, PR2) that allowed readings of volumetric soil water content at ten depths from 0.1m to 1.0m was installed at planting time in 2006 and 2007. In 2005 an access tubes for a time domain reflectometry (TDR) (Trime-FM) that allowed readings of volumetric soil water content at seven depths from 0.09m to 1.17m were used instead. Despite slight differences in the amount of soil integrated, both probes proved to be equivalent in their functionality.

Plant establishment and management

Experimental treatments were designed to represent a wide range of competitive environments where the maize was subject to varying levels of interspecific competition through the management of the relative time of emergence of the maize vs. the weeds. Three treatments plus control treatment (weed free maize) were established (MZ) (Table 1.2). In early emergence where weeds are expected to be highly competitive, weeds were planted before the maize and emerged approximately one week earlier (EE). In simultaneous emergence weeds emerged simultaneously with maize (SE). And, in late emergence where weeds are expected not to be competitive, weeds were planted after maize and emerged approximately one week after (LE). Some treatments were not present in all years; however the weed free maize and the simultaneously established *A.theophrasti*-maize treatments were included in every year.

Table 1.2 Experimental treatments and emergence dates (in parenthesis). AB-
A.theophrasti; MZ-maize.

Year	early emergence	simultaneous emergence		late emergence
	weedy treatment (EE)	weed free (MZ)	weedy treatment (SE)	weedy treatment (LE)
2005	---	MZ(6/7/05)	AB(6/7/05) MZ(6/7/05)	---
2006	AB(5/17/06) MZ(5/31/06)	MZ(5/31/06)	AB(5/29/06) MZ(5/31/06)	AB(6/13/06) MZ(5/31/06)
2007	---	MZ(5/29/07)	AB(5/30/07) MZ(5/29/07)	AB(6/13/07) MZ(5/29/07)

In all treatments where maize was present, maize cv. DK48-15 was planted in rows 0.75 m apart at a density of 8 plants m⁻². In the weedy treatments, velvetleaf (*A. theophrasti*) was sown with a garden-type push planter in two equally spaced rows in between the maize rows and thinned by hand after emergence to a density of 10 plants m⁻². After establishment all later emerging weeds were removed by hand, in order to maintain a uniformly-aged population and spatial arrangement of the plants. All plots were fertilized with N-P rates that supplied non-limiting amounts of those nutrients in both the maize and maize-weed treatments by applying extra fertilizer than what it would be normally recommended for maize alone in the maize-weeds treatments.

Measurements and data analysis

Soil moisture was measured daily or every other day in between rainfall events and was measured right after and before rainfall events to capture the start and end soil water content of a dry out period. For each access tube at least two readings per depth were taken, rotating the probe 90 degrees for the second reading to increase the accuracy of the measurements. Other measurements were taken weekly or every other week, as weather conditions permitted. Light interception was measured above and below the canopy with a 1m long sensor (Sunfleck ceptometer, Decagon Devices Inc.) under diffuse light conditions. Under these conditions the ratio of below:above photosynthetic active radiation readings (diffuse radiation transmittance coefficient, τ) is a good approximation of daily integrated light transmittance of the canopy, and since light is coming from all directions with approximately equal probability, leaf area index (LAI) estimates can be obtained directly without the assumption of a leaf angle distribution ($LAI = -\ln(\tau)$). Also on a weekly basis the height of the canopy for each species was measured, as well as the height, width and above ground biomass of selected plants later used to estimate

allometric relationships among these parameters.

At harvest, all maize plants in an area of 6.86 m² (3 meters linear length times 3 maize rows) were removed, the fresh weight of stover was registered, and cobs together with a stover subsample were oven dried at 70°C to determine the dry matter contents, stover yields, and grain yields of the maize.

After reviewing the entire dataset of soil moisture data, it was evident that significant variation in soil water recharge was observed among the access tubes due to soil surface sealing and micro-topography. The lack of a consistent recharge complicated the analysis using the soil water balance method, and therefore an alternative approach similar to the one adopted by Meinke et al. 1993 and Dardanelli, et al. 2004 was used. For each access tube, each measuring depth and for each dry-out event (period between rainfall events), an exponential decay function was fit to the data points ($FTSW = a \cdot e^{-b \cdot ETo_{cum}}$, equation 1); where $FTSW$ is the fraction of transpirable soil water or the fraction of water remaining between soil field capacity and permanent wilting point, ETo_{cum} is the cumulative reference evapotranspiration during the dry-out event estimated by the FAO-Penman-Monteith method (Allen, Pereira et al. 1998), and a and b are coefficients, with b being the rate constant for soil water extraction (fraction of the remaining $FTSW$ extracted in each time step per unit ETo_{cum}).

This fit was used to smooth the experimental error associated with the moisture readings themselves, to fill the gaps of missing daily soil moisture data between rainfall events and to extrapolate the daily soil moisture data until reaching the previous or next rainfall event. In this way daily soil moisture values were produced for each TDR tube during the entire growing season, and soil water extraction, as well as soil water recharge could be estimated by differentiating the time series. It is important to note that the rate of soil water extraction (coefficient b) is constant during the entire dry-out period and does not change as soil water is depleted from the soil, in contrast to a simple difference in soil water content after full soil recharge that it is commonly used as a measure of soil water

extraction in the literature (Meinke, Hammer et al. 1993).

Model simulations of each growing season and experimental treatments were also conducted. The model used is a version of the PNM (Precision Nitrogen Management) model (Sogbedji, van Es et al. 2006) that estimates soil processes within the root zone, including soil water infiltration and redistribution, soil temperature, soil organic matter mineralization, soil nitrogen losses by leaching and denitrification, and soil nitrogen transformations. In this model the soil was divided into 20 layers and all fluxes and transformations were estimated on a daily basis. The section of the model that simulates plant growth was modified to allow spatially explicit calculations of solar radiation for each individual plant using the algorithms of MAESTRA (Wang, Jarvis 1990). Photosynthesis was estimated hourly with an algorithm similar to the one used in Gecros (Yin XinYou, Laar 2005) which uses the Farquhar-vonCaemmerer model (Farquhar, Caemmerer et al. 1980, Yin, Van Oijen et al. 2004) and couples transpiration to photosynthesis through the stomatal conductance, assuming optimal stomatal conductance behavior (e.g. maximum stomatal conductance is determined by the photosynthesis demand for CO₂, and under water stress conditions it is reduced to match the soil water supply). Allocation of photosynthate was determined using allometric relationships of the form ($y = c \cdot x^b$) among shoot biomass and total plant biomass, and stem biomass and shoot biomass. The volume of soil exploited by each individual plant, which determines the amount of extractable soil water, was also estimated using allometric relationships with shoot biomass (Berger, McDonald et al. 2006). This model simulates the dynamic processes of growth and competition for resources (e.g. solar radiation, soil water, soil nitrogen), and produces estimates of water use, biomass accumulation, and grain yield. Individual processes within the model were parameterized with either field data from 2007 growing season (i.e. plant architecture and soil properties) or data from the literature (i.e. parameters associated with biomass partitioning, tissue nitrogen partitioning and photosynthesis estimations).

Crop water productivity (CWP) was calculated as the crop grain yield (kg ha^{-1}) measured in the field experiments divided by the season-long water use ($\text{m}^3 \text{ ha}^{-1}$). It was estimated using the season-long water use obtained from the field experiments or estimated from the model which also allowed us to estimate the CWP of the entire crop and each component of the crop (i.e. weeds and maize).

RESULTS

Water use and model validation

Due to the coupling between plant transpiration and carbon assimilation through stomatal conductance, total water use as well as the transpiration flux can be validated against biomass accumulation and *vice versa*. Since soil evaporation mainly draws water from the top 0 to 0.05m, we estimate that field measurements did not fully capture soil evaporation. That is because the TDR and PDP probes have inherent problems to accurately measure surface soil water and also because the first depth of measurement was 0.09 and 0.1m respectively. Field measured water extraction is considered to be equivalent to water use by the transpiration stream, with the assumption that root soil water uptake in the surface soil layer (0-0.05m) and soil water evaporation below the surface soil layer (0.05m) are small or at least cancel out. Figure 1.1 shows the modeled daily transpiration flux and the measured daily soil water extraction as calculated from field measurements for the three studied growing seasons. There is in general close agreement between the measured and observed data, and in particular there is close agreement during the two major drought events occurring between days 43 and 90 on 2005 and between 62 and 83 on 2006.

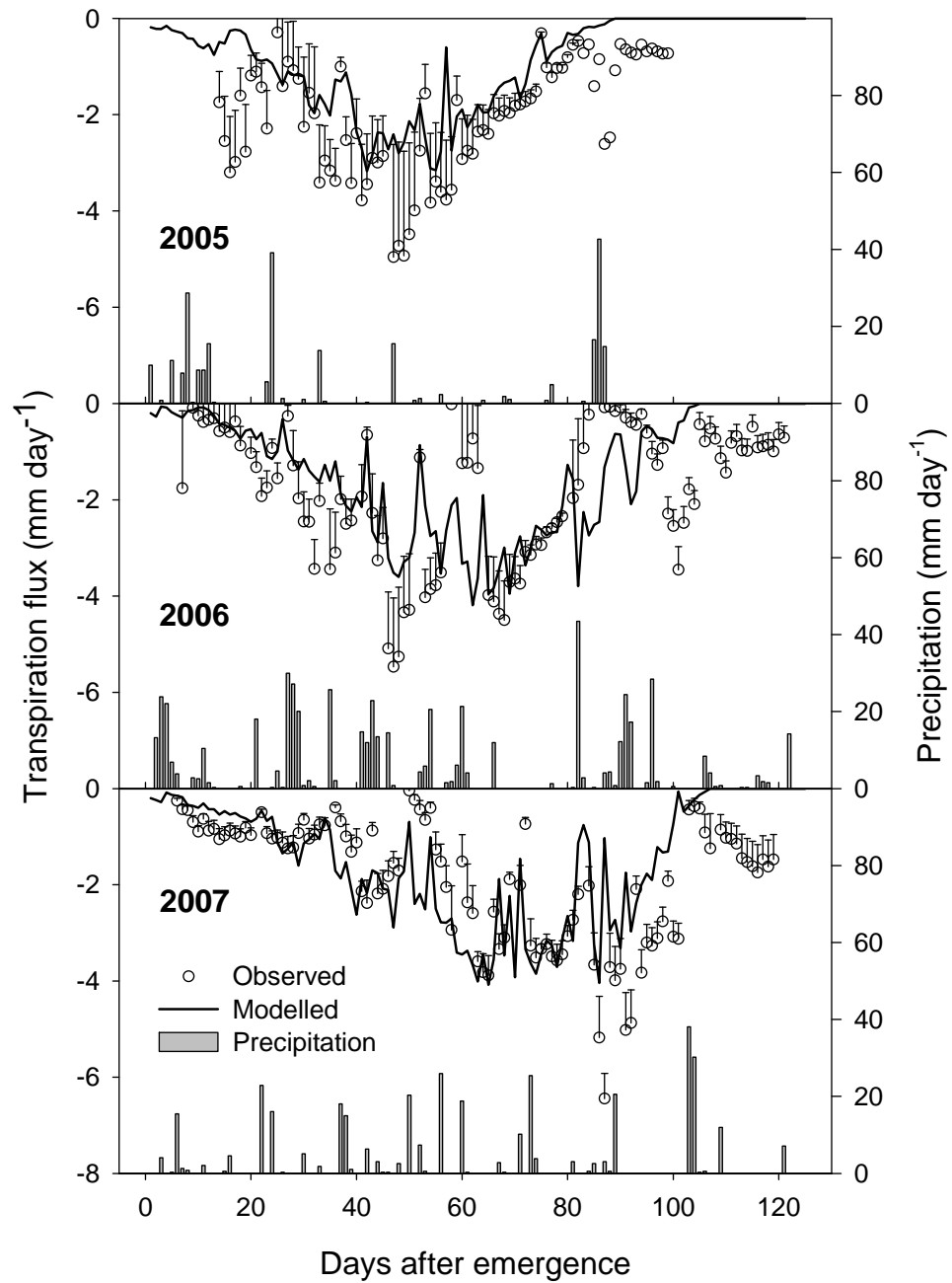


Figure 1.1 Mean transpiration flux for all treatments estimated from field measurements of soil moisture and corresponding estimated flux from the modeling exercise. Error bars indicate standard errors of the mean.

Maximum transpiration fluxes observed when the crop reached full canopy cover as well as season long soil water extraction (Figure 1.2) are low compared to observations made under climates with high atmospheric demand for water vapor (Zwart, Bastiaanssen 2004), but are consistent with the low atmospheric demand for water vapor and frequent rainfall events of the climate under which the current experiments were conducted. As the modeled totals presented in Figure 1.2 show, a large proportion of the total amount of water used during the cropping season was lost through evaporation, in particular in 2005 where crop development was lower (maximum maize leaf area index of 2.3). For conditions that ranged from atypically dry (2005) to atypically wet (2006), we found no evidence that the maize-weed mixtures had less total soil water, used more soil water through the growing season or had different rates of water extraction through the profile than the maize monocrop. As evidenced by the model simulations (bars on figure 2) the presence of weeds in the canopy shifted the partitioning of water transpired, reducing maize transpiration, but not the total amount transpired by the crop (maize + weeds). In the series of treatments EE, SE, LE, MZ, the dominance of maize in the canopy increased from EE to MZ, and so the share of the total amount of water transpired by maize. Only small increases in total water transpired can be suggested from the modeled simulations when *A. theophrasti* dominates in the canopy, probably due to the more inefficient, in terms of water use, C3 photosynthetic system.

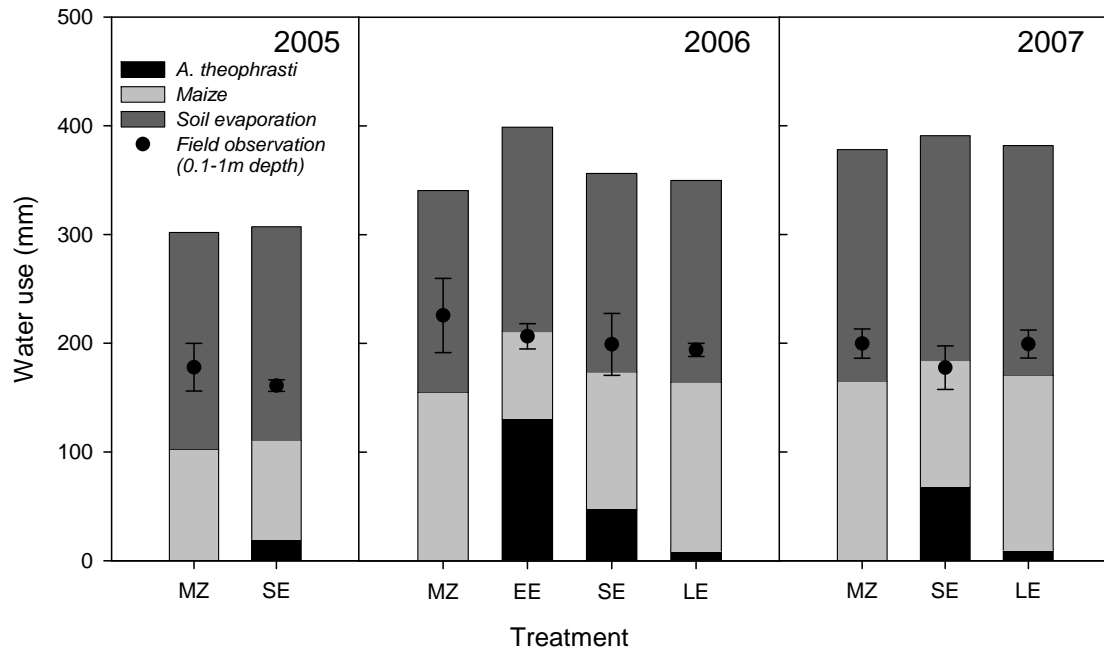


Figure 1.2 Observed season-long water use by the crop (0.1-1m, therefore does not fully include soil evaporation), and simulated season-long water use by the crop (transpiration and soil evaporation) including partitioning among sources of water. Error bars are standard errors of the means. (EE, early emergence; SE, simultaneous emergence; LE, late emergence)

Canopy development and water use by crops vs. weeds

In all three years, the crop achieved full canopy cover (>85% light interception) by the time maize was at anthesis (Figure 1.3), even when the dynamics of soil water use were different (Figure 1.1). After an initial 20-30 day phase where plants became established, the canopy rapidly developed to the point that it intercepted the majority of the incoming solar radiation, which was the driving force for transpiration. The presence of weeds significantly increased the amount of light intercepted early in the growing season during the short period of rapid canopy growth, shifting the time to reach maximum light interception approximately 5 to 10 days forward depending on the year (Figure 1.3). Nevertheless, the differences in light interception through the season were small considering that in the weedy treatments plant density doubled and leaf area index at maize anthesis increased by 1.13 on average.

Soil water extraction for the maize and maize-weeds treatments was compared by soil layers in order to test the possible differentiation of niches, where for example maize or weeds would extract water preferentially, therefore changing the dynamics of stored water extraction and possibly the ability to access water stored in unexploited regions of soil once it becomes scarce. Figure 1.4 shows the rate coefficients of soil water extraction (coefficient b in equation 1) for the MZ and SE treatments at selected dry-out periods that bracket maize anthesis occurring between 46-81, 65-79, 61-101 days after emergence for 2005, 2006 and 2007 respectively.

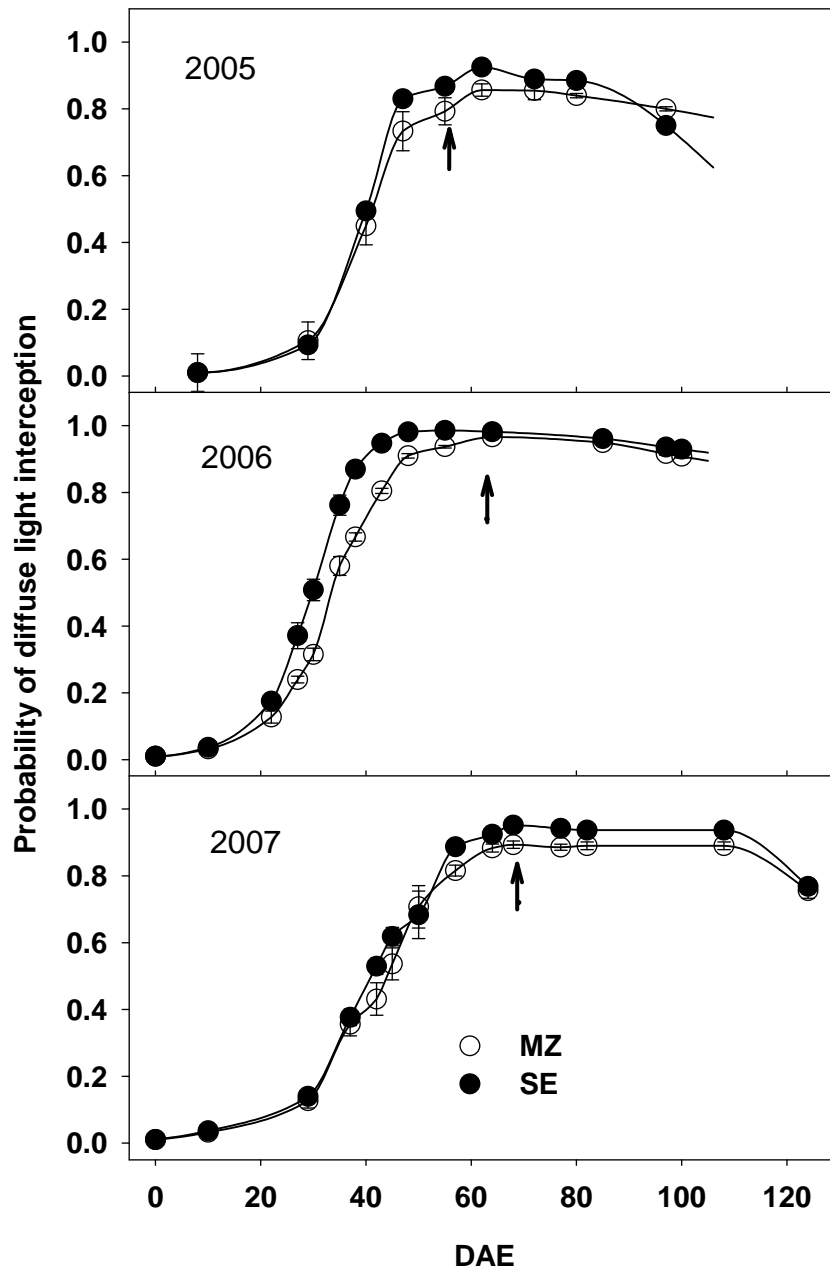


Figure 1.3 Canopy light interception indicated by the probability of diffuse light interception for the SE (maize and weeds emerging simultaneously) and MZ (maize weed free) treatments. Means and standard errors of the mean. Arrows indicate time of maize anthesis (n=5).

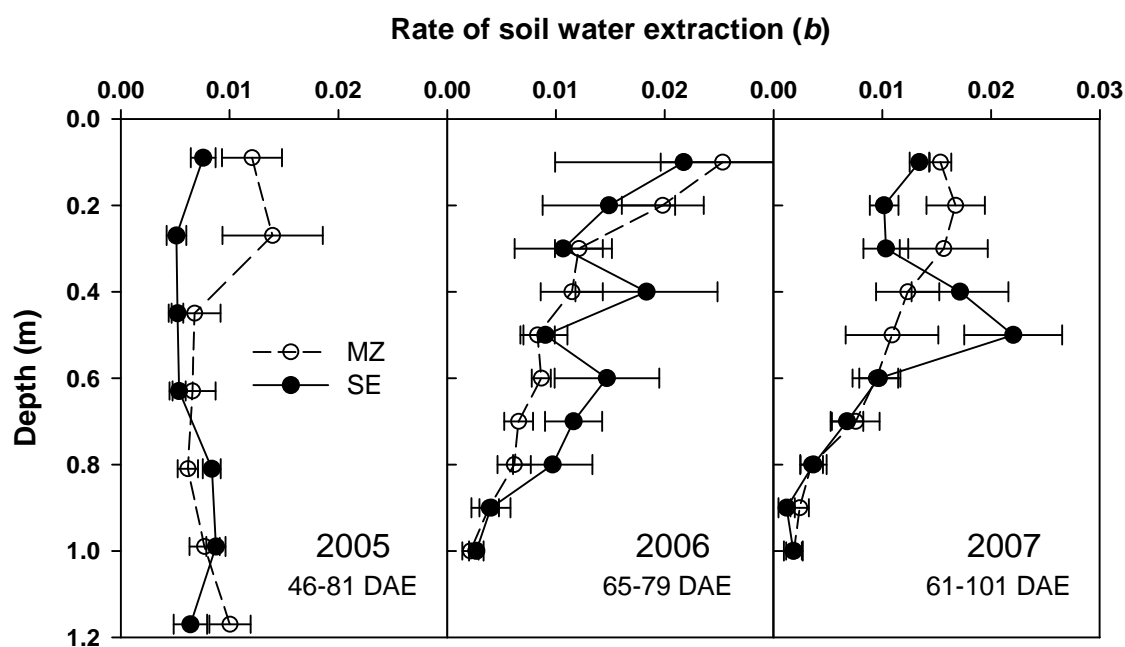


Figure 1.4 Rates of soil water extraction through the profile at observed on dry-out periods bracketing maize anthesis for the maize and maize weeds treatments. Error bars are standard errors of the mean (n=5).

Analysis of these profiles, as well as the analysis of similar profiles during other dry-out periods, shows that there is a tendency for the SE treatments to have slightly higher rates of extraction between 0.4m and 0.8m and slightly lower rates of extraction between 0m and 0.4m, however the variability associated with the measurements is relatively large and these differences were not statistically significant. These results do not suggest the creation of niches where the weed or crop preferentially extracts soil water.

Water stress and crop water productivity of weedy vs. weed free crops

Stomatal conductance was monitored around maize anthesis, to determine if maize plants were subject to the same levels of water stress in the weed free (MZ) and weedy treatments (SE). Figure 1.5 shows time series of stomatal conductance for maize measured with steady-state porometer in the field at noon for sunlit maize leaves on the upper part of the canopy, indicating no significant differences among weedy and weed-free treatments.

Since season-long water use did not differ significantly among treatments within each year (Table 1.3), crop water productivity (CWP, columns I and III) was mainly driven by the crop grain yield, and therefore was inversely related to yield loss due to weed competition. For example in 2006 CWP decreased as weed competition and yield loss increased (CWP order $EE < SE < LE < MZ$, yield loss order $MZ < LE < SE < EE$). Interestingly CWP in a dry year like 2005 was not different from CWP in 2006 or 2007, as both grain yield and season-long water use were reduced in similar proportion in 2005. Column II on Table 3 shows the CWP estimated using maize water transpiration estimated from the model output, indicating that CWP of the maize plants actually tended to increase with competition (EE vs. MZ in 2006 and SE vs. MZ in 2007), probably caused by increased water use efficiency at the leaf level due to partial shading.

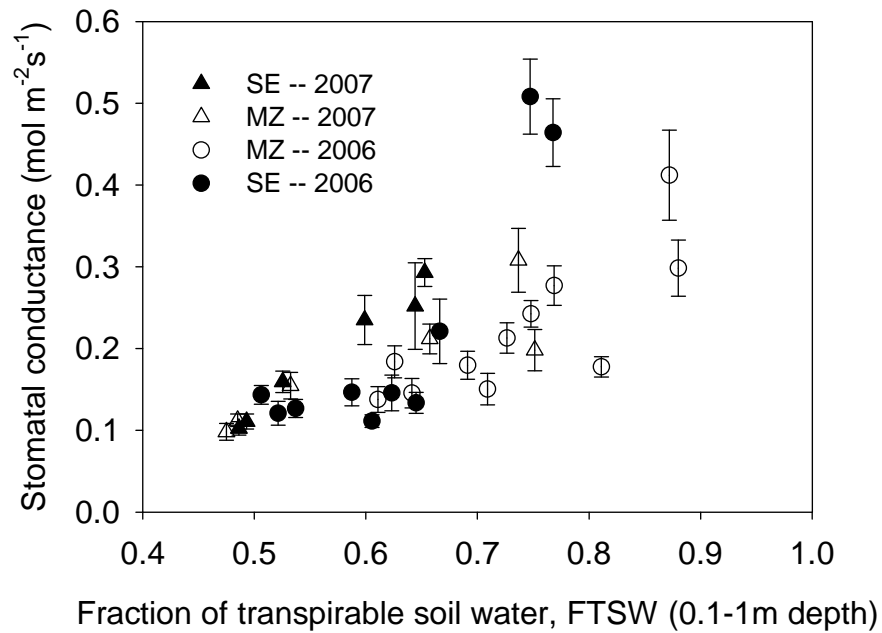


Figure 1.5 Mean maize stomatal conductance measured in the field at noon in the maize and maize-weeds treatments, and mean 0.1-1m depth soil moisture content (FTSW) measured in the corresponding plots. Error bars are standard error of the means.

Table 1.3 Mean and standard errors of the mean maize harvest index (grain yield/total above-ground biomass), yield loss (1-[grain yield weedy treatment/grain yield control]) and crop water productivity estimated using field observed water extraction (I), model estimated water transpiration for maize (II) and model estimated water extraction (transpiration+soil evaporation) for crop (maize+weeds) (III). Means followed by the same letter are not statistically different according to multiple t test with $\alpha=0.05$.

Year	Treatment	Maize harvest index				Yield loss	CWP											
							I				II				III			
		%									Kg m ⁻³							
2005	SE	51	±	1.5	a	18	4.9	±	0.36	a	8.7	±	0.7	a	2.6	±	0.21	a
	MZ	54	±	3.7	a	0	5.6	±	1.09	a	9.4	±	1.4	a	3.2	±	0.47	a
2006	EE	51	±	4.9	b	44	3.9	±	0.49	b	10.0	±	0.57	a	2.0	±	0.12	c
	SE	54	±	2.0	ab	25	5.3	±	0.12	ab	8.6	±	0.47	b	3.0	±	0.17	b
	LE	59	±	1.1	a	7	7.3	±	1.15	a	8.6	±	0.23	b	3.8	±	0.10	a
	MZ	58	±	1.5	a	0	7.4	±	0.27	a	9.3	±	0.27	ab	4.2	±	0.12	a
2007	SE	58	±	2.4	a	11	6.4	±	0.86	a	9.2	±	0.40	a	2.7	±	0.12	a
	LE	54	±	3.7	a	10	5.6	±	0.89	a	6.7	±	0.79	b	2.8	±	0.33	a
	MZ	56	±	1.8	a	0	5.9	±	0.59	a	7.3	±	0.38	b	3.2	±	0.16	a

DISCUSSION

Water use and competition for resources as a dynamic process

Plant growth is a dynamic process, as plants acquire resources (i.e. light) they grow and further enhance their capacity to acquire more resources. When the availability of resources is less than the requirements (resources become limiting) plants compete among each other and restrict their use of resources and growth accordingly. In monospecific stands (i.e. crops) plants usually compete among each other and individual growth gets restricted, in multispecies stands (i.e. crop-weeds) individual plant growth gets restricted as well and therefore the proportion of the total crop biomass producing harvestable yield is reduced. The dynamics of growth and resource acquisition, as well as the total amount of resources available are therefore extremely important in defining the outcomes of competition (Baldwin 1976). For example, if and when full canopy cover is established the majority of the solar radiation is intercepted by the crop, the amount of water transpired by it depends on the atmospheric demand for water vapor, and the water status of the root zone. Results from 2005, 2006 and 2007 confirm this, and suggest that after full canopy cover is achieved, soil water reserves will be depleted at a similar rate in both weedy and weed-free treatments. When the presence of weeds accelerates canopy closure, soil water reserves will be depleted earlier compared to a weed-free crop. In this experiment, differences in canopy light interception between SE and MZ were small during most of the season except for a short period of time (e.g. 5-10 days) during the rapid growth phase when interception in the mixed stand was up to 20% higher (Figure 1.3). Figure 1.6 summarizes the dynamics of light interception (directly linked to evaporation) and soil profile exploration. It also highlights that in the context of this

study and a climate characterized by frequent recharge of the soil profile: i) unless a dry spell occurs during the phase of rapid growth (phase 2 in Figure 1.6) the differences in soil water extraction between the weedy and weed-free treatments will be small, ii) if there are no stress events before full canopy cover (phase 3 in Figure 1.6), the presence of weeds would not deplete the storage of water to a greater degree than the weed free crop would, and iii) during the initial growth phase (1 in Figure 1.6) water is extracted from a small portion of the soil profile and therefore could be fully recharged with small rainfall amounts. It arises from this analysis that the presence of weeds is only likely to influence the soil water balance and drive the crop into stress if a dry spell occurs within a relatively narrow period of time. This complement the general statement often found in the literature that weeds always deplete the stocks of soil water thereby inducing or exacerbating crop water stress (Turner 2004).

There are at least three scenarios not observed in this study under which the presence of weeds may cause crop water stress: i) when the weed infestation is large enough to create significant differences in canopy cover early in the season, ii) when full canopy cover is never reached, and iii) when recharge is insufficient to compensate for any differences in soil water status that develop early in the growing season. These latter two scenarios are commonly occurring in water limited environments and Mediterranean type climates, for which extensive research has been undertaken to improve CWP, and are the source of a large proportion of the available literature on crop water use, CWP and management practices that alter them (Turner 2004, Turner, Begg 1981). Under a climate like the one found in the US Northeast and for summer crops, these scenarios are not that common, and therefore it is unlikely that the presence of weeds would increase the chances of a maize crop to become water stressed.

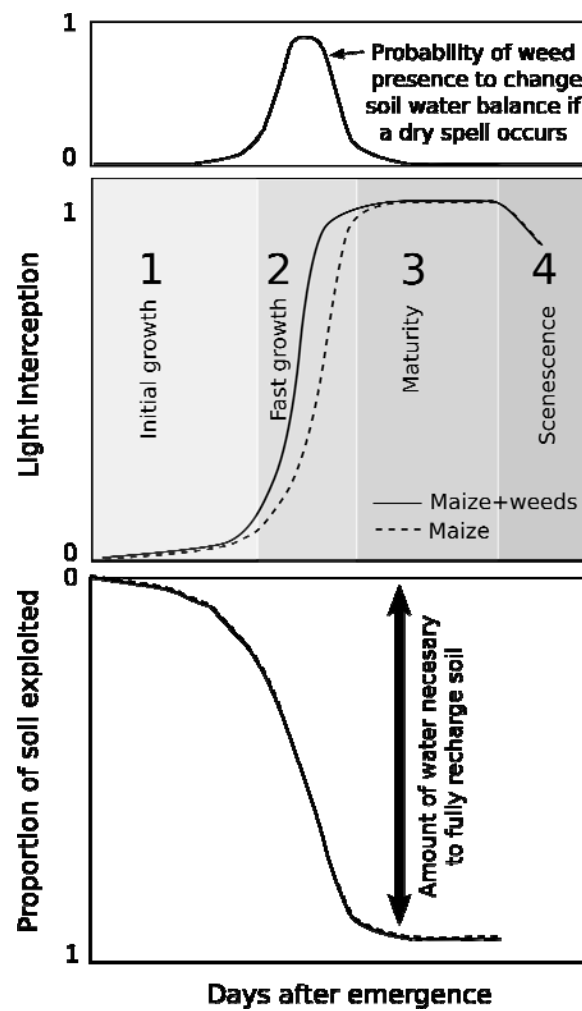


Figure 1.6 Schematic diagram of the main drivers of water use/storage over time and their interrelationships as determinants of the likelihood for the presence of weeds to drive the crop into water stress.

Is maize in a weedy crop more stressed than maize in a weed free crop?

Regardless of the discussion in the previous section about whether the presence of weeds drives the crop into water stress or not through the depletion of the soil water reserves, an important question is: once the crop is under water stress, is maize more stressed when weeds are present compared to when weeds are not present? Time series monitoring of stomatal conductance in the field and model results suggest that maize was no more water stressed in the weedy treatments (Figure 1.5). This similarity in stomatal conductance indicates that maize plants in the weedy treatments experience the same level of water stress as those in maize monoculture. This is likely the result of similar exploration of the soil profile (Figure 1.4) and similar scaling among soil exploration and above-ground biomass (transpiring leaves). This study indicates that it is the low photosynthetic rate due to reduced light interception that is the main cause of the yield loss, in contrast to the low photosynthetic rate due to water stress *per se*. This data further suggests that in a hypothetical case where weeds completely overtop the maize and high yield loss are expected, the maize plants will intercept a small proportion of the total available solar radiation and will be responsible for a small proportion of the total transpiration as well, but they would not experience higher levels of water stress.

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CHAPTER 2

THE EFFECT OF SIZE INEQUALITY AND SPATIAL ARRANGEMENT OF PLANTS ON COMPEITION AND RESOURCE CAPTURE

ABSTRACT

Among annual plants competition impacts the dynamics of plant growth and influences the final biomass and seed yield. The objective of this study was to test, through field experiments and an individual based model, the effects of size inequality and plant spatial arrangements on the competitive relationships among annual plants, the evolution of plant sizes distributions, and the ability of plants to capture resources. The model, which estimates light interception, photosynthesis, respiration, growth, photosynthate allocation and root growth at the plant level, allows individual plants to compete for resources, including solar radiation and soil water and nitrogen. Resource use was largely dependent on the size of the plant, and most importantly on the relative position of the plant within the canopy. Taller plants with greater leaf area utilized a proportionally larger share of available resources. Model simulations allowed us to examine the effects of resource scarcity on the dynamics of growth of individual plants and the formation of hierarchies within the canopy and *vice-versa*. Plant size distributions for each species cohort became more positively skewed as time progressed since the largest plants in the cohort capitalized on their advantage. This effect was greater as availability of resources increased, thus allowing more growth, or when a species cohort grew more quickly relative to another species cohort due to timing of emergence or spatial proximity. This study demonstrates that species cohorts do not modify their competitors' ability to capture resources independent of their

position within the canopy. The dynamic nature of resource supply and resource capture and growth among competing species, as well as sensitivity to initial conditions, result in highly variable competitive outcomes in these systems.

INTRODUCTION

In natural as well as managed ecosystems, competition for resources is one of the main determinants of a plant's success within the plant community and also one of the main drivers of successional change. A large number of studies have considered the effects of competition for resources on plant community diversity (Purves, Pacala 2008), plant community productivity (van Wijk 2007) and the yield loss of crops or pastures (Cousens 1985, Deen, Cousens et al. 2003, van Ittersum, Leffelaar et al. 2003). Both experimental (Cousens 1985, Fahey, Battles et al. 1998) and modeling (Deen, Cousens et al. 2003, Breckling, Middelhoff et al. 2006, Yokozawa 1999, Hara, Wyszomirski 1994) approaches have been used, with the latter category including stochastic (Purves, Pacala 2008, Pacala 1986), individual based (Breckling, Middelhoff et al. 2006), patch or gap (Moorcroft, Hurtt et al. 2001, Pacala, Canham et al. 1996, Wang, Jarvis 1990) and dynamic simulation models (van Ittersum, Leffelaar et al. 2003). Modeling has been used to expand on the results obtained in experiments and to analyze the effects of multiple factors that are usually involved in resource competition among plants, which are hard to impose or observe in their full range of possible variability. Most of the models have relied on empirical relationships to determine the capacity to capture resources (e.g. distance to the nearest neighbor, zone of influence) in an effort towards parsimony, have made simplifying assumptions about the composition of the plant community or the sizes of the plants. Very few

models include mechanistic approaches that consider light interception, plant development, or partitioning and root growth simultaneously, even though the outcomes of competition may be highly dependent on the interaction among all these processes involved in resource capture (Craine 2005). Furthermore, both experimental and modeling studies have not fully addressed the interrelationship between above and below ground resource capture and how it affects an individual plant's success under contrasting environments. For example, competition for above ground resources (chiefly light) has been considered to be size asymmetric (i.e. larger individuals acquire an even larger shares of the contested resource with respect to their size) (Freckleton, Watkinson 2001), but it is unclear that this advantage holds under all environmental conditions. Under water stress conditions, large plant size which confers enhanced capacity to intercept light could turn into a disadvantage because it also increases the amount of water needed to meet transpiration demand.

Individual based models offer the opportunity to explore the effects of individual plants on the population, recognizing that the interactions among individuals are responsible for population level emergent properties (Breckling, Middelhoff et al. 2006). Such models make it possible to represent the structural-functional relationships of plant communities in a coherent way with respect to the ecological knowledge, making mechanistic models more realistic as model processes and parameterizations are directly linked to the actual individual organism instead of an average assumed individual organism (Hara, Wyszomirski 1994). For this reason individual based models are usually less sensitive to initial conditions and parameterizations compared to deterministic mathematical models, as the overall behavior emerges from the overlay of activities of individuals interacting at a lower level of organization (Breckling, Middelhoff et al. 2006). Only a few of the plant competition models that recognize the existence of individuals simultaneously utilize

physically based approaches to determine the use and share of the resources pool acquired by each individual plant (Evers, Vos et al. 2007, Wu, McGechan et al. 2007). That is probably due to the computational and parameter requirements, which complicate calibration, analysis and simulation of large ecologically relevant scenarios.

The objective of this paper is to test, through field experiments and an individual based model, the effects of size inequality and plant spatial arrangements on the competitive relationships among plants, the success of individuals, the evolution of plant sizes distributions and the ability of individual plants to capture resources under a range of possible climatic conditions found for annual crops in a temperate region such as the Northeastern US.

METHODS

The rationale for developing a model that represents individual plants of different species was to quantify how the average sizes, and distribution of sizes, changes upon changes in resource availability, as well as to understand how the dynamics of growth influence competitive outcomes. The emphasis was in developing a mechanistically rich model, using robust calculations for light interception, photosynthesis, biomass allocation and root growth. The model does not represent the individual plant organs (i.e. leaves or root segments) in 3D (Evers, Vos et al. 2007), which would have required larger computation times, yet it includes greater complexity than previous models of crop-weed competition (Deen, Cousens et al. 2003, Kropff, Weaver et al. 1992, Lindquist 2001b) that ignore spatial arrangements in the field and size distributions of the plants. Results from the simulations were

compared to field observations when possible to validate the model, and additional field measurements were collected to contribute towards the understanding of the dynamics of growth and competition in the field experiments.

Canopy light interception, photosynthesis and transpiration

The solar radiation interception and photosynthesis algorithms are described in greater detail elsewhere (Wang, Jarvis 1990, Wang, Jarvis et al. 1991, Yin XinYou, Laar 2005) and will only be summarized here. The amount of radiation intercepted by individual plants in a canopy was estimated using the algorithms of MAESTRA (Wang, Jarvis 1990), which use a ‘turbid medium’ approach to estimate radiation interception at discrete points for foliage elements that are assumed to be randomly distributed within the volume enclosed by a plant’s crown. The code was slightly modified to handle multiple species; each species leaf optical properties, vertical and horizontal leaf area distribution within the crown and parameters for the photosynthesis model can be uniquely defined.

Photosynthesis was estimated hourly at all of the discrete points within each plant’s crown for which radiation interception was calculated and then integrated over the plant and over the day to obtain daily net CO₂ assimilation for each plant. The algorithm used to calculate photosynthesis is similar to the PPHTR-APHTR algorithm of Gecros (Yin XinYou, Laar 2005) which uses the Farquhar-von Caemmerer model to calculate photosynthesis (Yin, Van Oijen et al. 2004, Farquhar, Caemmerer et al. 1980) and couples transpiration to photosynthesis. When soil water supply is sufficient to meet potential transpiration (ET_o), the rate of photosynthesis is used to determine stomatal conductance, which in turn is used to calculate actual transpiration (ET_a); in this case $ET_a/ET_o=1$. In contrast, when the soil water supply is not sufficient to meet

potential transpiration ($ETa/ETo < 1$), actual transpiration is used to estimate stomatal conductance and then the actual rate of photosynthesis. This method assumes optimality in water use, recognizing that stomatal aperture is adjusted to maximize carbon gain with respect to water loss (Schymanski, Roderick et al. 2008). This approach avoids the parameterization of stomatal conductance, but requires a function linking soil available water and plant available water (ETa/ETo). For this purpose we used a function proposed by Sinclair (2005) that yields an approximate relationship between ETa/ETo and soil water potential after eliminating minor terms through a theoretical analysis of plant water uptake (Sinclair 2005) (Eq. 1).

$$ETa/ETo_j = 1 - \frac{\sum_i \psi_{soil_i} w_{ij}}{\psi_{leaf}} \quad (1)$$

where ψ_{soil_i} is the soil water potential in soil layer i , zoi_{ij} is the volume of the root zone of influence of plant j in layer i , and ψ_{leaf} is the leaf water potential, which is assumed constant ($\psi_{leaf} = 1.5 \text{ MPa}$). Before applying Eq. 1 and in order to scale up from the soil layers to the entire soil profile, the soil water potential in each soil layer was weighted by the proportion of root zone of influence in each soil layer (Eq. 2).

$$w_{ij} = \frac{zoi_{ij}}{\sum_i zoi_{ij}} \quad (2)$$

After calculating photosynthesis rates with the ETa/ETo values obtained in Eq. 1, the actual amount of water to be extracted by a plant to satisfy actual transpiration (ETa_j) was apportioned to the different soil layers according to a weighting factor that considers the soil water content (ETa/ETo_i from Eq. 3) and the volume of the root zone of influence (w_{ij}) in each soil layer i (Eq. 3 and 4).

$$ETa/ETo_i = 1 - \psi_{soil_i} \psi_{leaf}^{-1} \quad (3)$$

$$ETa_{ij} = ETa_j \frac{ETa/ETo_i w_{ij}}{\sum_i ETa/ETo_i w_{ij}} \quad (4)$$

Plant respiration is estimated on a daily basis with procedures similar to those described in (Yin XinYou, Laar 2005). In this framework, respiration is divided in six components associated with the respiratory costs of growth, nitrate uptake, ammonia uptake, other nutrient uptake, phloem loading and maintenance respiration, where the first three mentioned components are the primary ones.

Allocation and plant architecture

Photosynthate is allocated on a daily basis to the different plant organs (i.e. root, stem, and leaf) assuming allometric growth (Weiner 2004). Therefore the share of photosynthate partitioned to each organ changes with the size of the plant. This is described by the differential equations 5 and 6:

$$\frac{\partial w_{shoot}}{\partial w_{total}} = \alpha_{shoot} \frac{w_{shoot}}{w_{total}} \quad (5)$$

$$\frac{\partial w_{leaves}}{\partial w_{shoot}} = \alpha_{leaves} \frac{w_{leaves}}{w_{shoot}} \quad (6)$$

where w_{total} is the total plant biomass, w_{shoot} is the total above-ground biomass (stem+leaves), w_{leaves} is the biomass of the leaves and α_{shoot} and α_{leaves} are the corresponding coefficients for the allometric relationships between shoot and total

plant biomass ($w_{shoot} = \beta_{shoot} w_{total}^{\alpha_{shoot}}$) and leaf biomass and shoot biomass ($w_{leaves} = \beta_{leaves} w_{shoot}^{\alpha_{leaves}}$).

Plant architecture was also modeled assuming allometric relationships between the total plant biomass (w_{total}) and height (h) and crown width (r) (Eqn. 7 and 8):

$$h = \beta_{height} w_{total}^{\alpha_{height}} \quad (7)$$

$$r = \beta_{width} w_{total}^{\alpha_{width}} \quad (8)$$

where β_{height} , β_{width} , α_{height} and α_{width} are species specific allometric coefficients. Increments in height or width due to plasticity responses (i.e. induced by shading) are known to increase the values of β (Weiner, Thomas 1992) which results in an upward shift in the ‘allometric growth path’ while maintaining constant values of α . However, in this model we opted for selecting a single value of β representative of plasticity-induced plants (plants under intense competition).

Nitrogen allocation to different plant components (roots, stem, green leaves, senescent leaves and seeds) is based on a set of rules that, i) prioritized the sink strength of some components over others based on maximum and minimum nitrogen contents, ii) depended on the overall availability of nitrogen in the root zone, and iii) were a function of the growth stage of the plant (Figure 2.1). This procedure is similar to the one adopted by Jamieson, et al. (2000) and Sinclair, et al. (1995), with the difference that the rules used in this model allowed simultaneous vegetative and reproductive growth. During reproductive growth, the model allows nitrogen to be remobilized from senescing leaf tissues in order to satisfy the requirements of the growing tissues. Additional leaf senescence according to the mentioned allocation rules occurred upon scarcity in the supply of nitrogen, as needed during vegetative or reproductive growth.

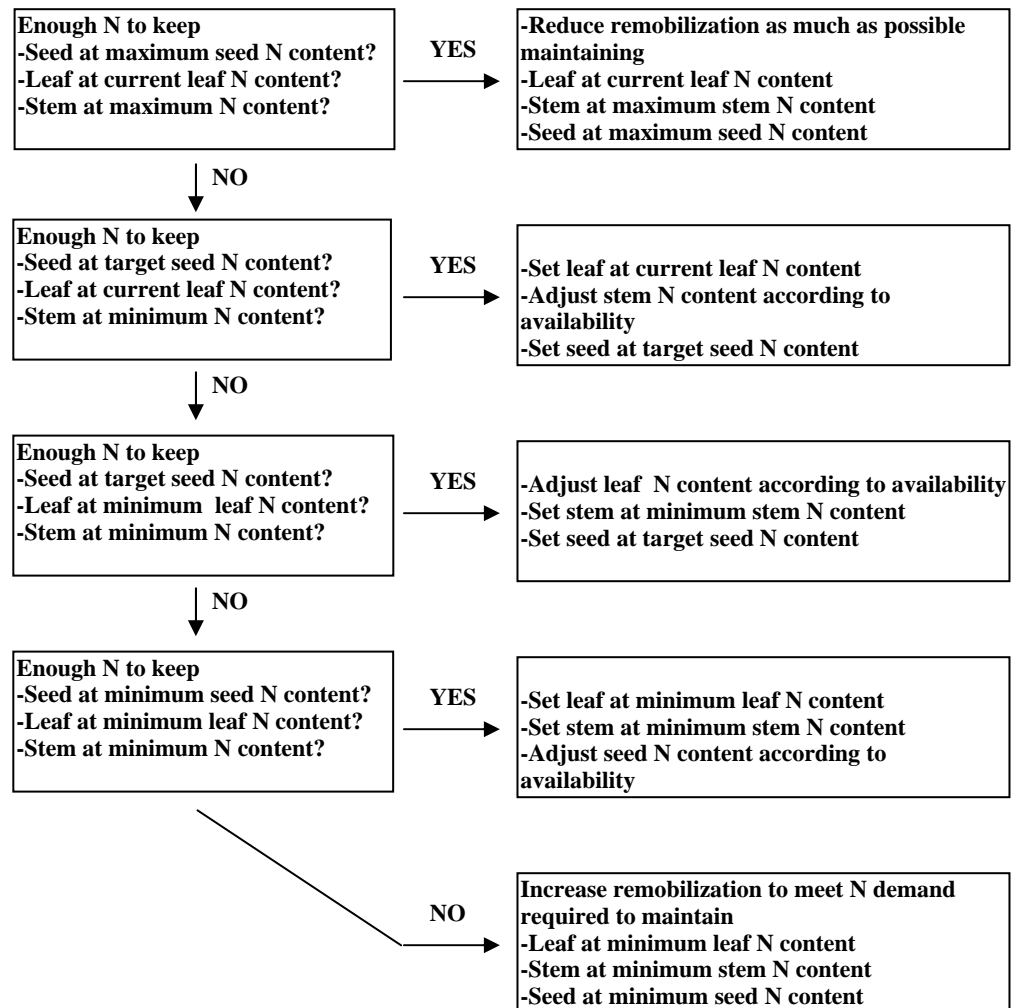


Figure 2.1 Allocation rules for plant nitrogen.

Root growth

Scaling relationships between above ground biomass and ZOI were used to estimate the volume of soil exploited by each plant and consequently the share of soil resources available to each plant (Berger, McDonald et al. 2006). The lateral expansion of the root system (l) was estimated from a scaling relationship with the above ground biomass (w_{shoot}) (Eqn. 9) until a limit to lateral expansion was reached, while vertical expansion (d) was estimated according to thermal time (gdd) until roots reached a maximum rooting depth (d_{max}) (Eqn. 10).

$$l = y_0 + a(1 - e^{-b \cdot w_{shoot}}) \quad (9)$$

$$d = \min(d_{max}, 5 \cdot e^{c \cdot gdd}) \quad (10)$$

where a , b , and c are empirical parameters, y_0 is the initial lateral expansion and d_{max} is the maximum rooting depth. This approach was developed on the basis of our field measurements of lateral and vertical root growth as well as field observations of soil water extraction.

The lateral expansion of the root system of individual plants was estimated for each soil layer and was used to calculate the root zone of influence volume, in order to derive the share of soil resources corresponding to each individual, assuming a radial pattern of root expansion (i.e. each root system layer is represented by a cylinder).

Soil processes

A version of the LEACHN model (Hutson, Wagenet 1991) called PNM (Sogbedji, van Es et al. 2006) was used to estimate soil processes within the root zone, including soil water infiltration and redistribution, soil temperature, soil organic matter mineralization, soil nitrogen losses by leaching and denitrification, and soil nitrogen transformations. In this model the soil was divided into layers and all fluxes and transformations were estimated on a daily basis.

Study site

Field experiments were conducted in Ithaca, NY (42° 27' N, 76° 27' W) during the 2005-2006-2007 growing seasons (May – August). The soil at the field site is a Williamson silt loam soil (coarse-silty, mixed, active, mesic Typic Fragiudept) with soil bulk densities at 10, 30 and 50 cm depth of 1.27 ± 0.02 , 1.47 ± 0.03 , 1.52 ± 0.02 g cm⁻³. The plots were arranged in a randomized complete block design with three replicates in 2005 and five replicates in 2006 and 2007. Experimental treatments were: weed free maize (cv. DK48-15) (MZ); a mixture of maize and velvetleaf (*Abutilon theophrasti*, M.), with velvetleaf emerging approximately one week before (EE), simultaneously (SE) or one week after the maize (LE). In each plot (plot size 4x3m), an access tube for a portable dielectric probe (PDP) (Delta-T, PR2) that allowed readings of volumetric soil water content at ten depths from 0.1m to 1.0m was installed at planting time in 2006 and 2007. In 2005, access tubes for a time domain reflectometry system (TDR) (Trime-FM) that allowed readings of volumetric soil water content at seven depths from 0.09m to 1.17m were used instead. Access tubes were installed at one third of the maize inter-row distance within the center row of

each plot, and soil moisture was monitored in between rainfall events daily or every other day. Daily weather data was obtained from a station located less than 0.5 km from the site.

All species were sown with a garden-type push planter. For the monoculture treatments, plants were established in rows 75 cm apart. The mixtures had the same spatial arrangement of maize plus two rows of velvetleaf in the center, 0.25m apart from the maize. After emergence all plots were thinned by hand to the desired plant density (10 plants m^{-2} for the weeds and 8 plants m^{-2} for maize), which was maintained through hand weeding until the end of the experiment.

Field measurements, model calibration and simulations

Soil moisture content was measured every day when possible, particularly following rainfall events or, when rain was forecasted, before the rainfall event to capture the full length of each dry period. To obtain daily values of soil water extraction for each tube and soil layer, an exponential decay function was fit to soil moisture (expressed as plant available water on a 0-1 scale) against cumulative reference evapotranspiration. Soil moisture as well as final maize grain yield and biomass accumulation at anthesis were used to assess model performance. Due to the coupling of water use and photosynthesis in the model, time series of soil water extraction can be used to validate the photosynthesis sub model, and gain confidence in dry matter and leaf area simulations.

Plant height was monitored weekly, measuring individual height of 5 plants per species per plot in 2007 and measuring the maximum height of the canopy for each species in 2005, 2006 and 2007. At the same time plants were harvested through the season measuring individual height, width and dry weight in order to obtain allometric

relationships among them (Table 2.1).

In order to measure the vertical leaf area distribution of each species at the time of maize anthesis, a two-measurement procedure combined with destructive harvesting was conducted in three out of five blocks in 2006 and 2007. First, photosynthetically active radiation (PAR) was measured using a 1m long sensor at 0.2m intervals from the soil surface to the top of the canopy under diffuse light conditions. Then *A. theophrasti* plants were removed and a second series of light measurements was conducted at the same heights and locations. Each set of PAR readings allowed us to estimate the vertical distribution of leaf area density (LAD) and, through the differences between the first and second set of measurement, the LAD distribution of each species. To improve the results and avoid the accumulation of errors, the difference was taken between the LAD values obtained in the second reading and values estimated through fitting equation 11 to the first LAD readings. Equation 11 describes the vertical leaf area density distribution with one parameter (Olesen, Hansen et al. 2004),

$$\gamma(x) = (a + 1)(a + 2) \frac{x^a}{h^{a+1}} \left(1 - \frac{x}{h} \right) \quad (11)$$

where $\gamma(x)$ is the leaf area density at height x , h is the canopy height, and a describes the relative vertical distribution of canopy area. Large values of a correspond to a negatively skewed distribution, while $a=1$ corresponds to a zero-skewed distribution. Values of a were used to compare changes in vertical distribution of leaf area of maize and *A. theophrasti* plant communities across treatments.

Table 2.1 Major model parameters, values, and sources.

Parameter	Maize	A. <i>theophrasti</i>	Units	Description	Source
Photosynthesis					
E_{Jmax}	77900	85000	J mol ⁻¹	Activation energy for J _{max}	a
X_{vcn}	65	55	umol g ⁻¹ s ⁻¹	Slope of linearity between Vc _{max} and leaf N	a
X_{jn}	130	110	umol g ⁻¹ s ⁻¹	Slope of linearity between J _{max} and leaf N	a
Np	0.25	0.4	g m ⁻²	Minimum photosynthetically active leaf N	b
Θ	0.7	0.7	--	Convexity of electron transport limited photosynthesis response curve	b
Allocation and plant architecture					
α_{shoot}	1.133	1.133	--	Shoot-total biomass scaling coefficient	c
α_{leaves}	0.863	0.865	--	Leaves-shoot biomass scaling coefficient	c
α_{height}	0.485	0.5929	--	Height-above ground biomass scaling coefficient	c
β_{height}	0.066	0.13	m	Height-above ground biomass scaling constant	c
α_{width}	0.268	0.4212	--	Width-above ground biomass scaling coefficient	c
β_{width}	2.15	3.18	m	Width-above ground biomass scaling coefficient	c
LA	0.014	0.001	m ²	Initial leaf area at 2 leaf count	c
Nitrogen balance					
leafN _{max}	2	3	g m ⁻²	Maximum leaf nitrogen content	d
leafN _{min}	0.55	0.55	g m ⁻²	Leaf nitrogen content that triggers senescence	d
leafN _{senescence}	0.4	0.4	g m ⁻²	Nitrogen content of senesced leaves	d
stemN _{max}	15	15	g kg ⁻¹	Maximum stem nitrogen content	d
stemN _{min}	2.5	2.5	g kg ⁻¹	Minimum stem nitrogen content	d
seedN _{max}	17	17	g kg ⁻¹	Maximum seed nitrogen content	d
seedN _{target}	14.5	14.5	g kg ⁻¹	Target seed nitrogen content	d
seedN _{min}	11	11	g kg ⁻¹	Minimum seed nitrogen content	d
Phenology					
GDD _{anthesis}	795	795	GDD	GDDs to anthesis (°C)	c
GDD _{grain}	533	533	GDD	GDDs for grain fill (°C)	c
tbase	8	8	GDD	Base temperature for GDD calculation (°C)	c
a	(Massad, Tuzet et al. 2007, Medlyn, Loustau et al. 2002)				
b	(Muchow, Sinclair 1994)				
c	Field experiments				
d	(Muchow, Sinclair 1994, Lindquist 2001a)				

The model was parameterized with data obtained in harvest of plants outside the experimental plots in 2006 and 2007, and from the literature. Table 2.1 lists a subset of the major model parameters, their values and the sources. The number of parameters is large, and it has been suggested that this model may be over parameterized (Medlyn, Robinson et al. 2005), however a number of validation checks, such as field measured stomatal conductance, light interception, leaf area, biomass and yield give confidence to the overall structure. Furthermore, the output of the model is based in the basic processes like photosynthesis, which is linked directly to transpiration, thus the model structure allows the validation of the parameterization.

Three sets of simulations were conducted. In the first set, the conditions of field experiments during 2006 were used, and EE, SE and LE treatments were simulated. The objective of this set was to compare model output to field data, and to use the model to derive field parameters not directly measured (i.e. partitioning of water use among plants). In the second set of simulations three scenarios were simulated, a) one representing the growing conditions (plant density, soils and weather) of 2006, b) a shortage of soil nitrogen (fertilization at planting 33 kgN ha^{-1} instead of 165 kgN ha^{-1}) and c) a drought (precipitation reduced to 1/3 the amount observed in 2006 while maintaining its distribution). The objective was to evaluate the effects of resource availability on the intensity and dynamics of competition among plants. Finally a third set of simulations was conducted to understand the effects of the spatial arrangement of plants on the dynamics of growth and competition for resources. Four scenarios were simulated with different arrangements of *A. theophrasti* plants: a) rows at $1/3$ and $2/3$ of the inter-row space, b) rows at $2/6$ and $5/6$ of the inter-row space, c) rows at $1/12$ and $11/12$ of the inter-row space, and d) a random uniform arrangement of plants.

RESULTS

Field observations of the formation of canopy hierarchies and the dynamics of growth

Close monitoring of individual plants in the field allowed us to track the dynamics of growth of the plant population, and to monitor the formation of hierarchies within the canopy. With height as a measure of plant size and competitive ability, the evolution of height distributions gives insights on how plants are competing. As shown in the probability density plots presented in Figure 2.2, the variance of each species cohort (maize or *A. theophrasti*) increased over time. During the initial stages of plant development, growth tends to be proportional to plant size (Weiner, Thomas 1992). Therefore when plants within a species cohort grow at the same relative growth rate but initial size disparities are present, size variance tends to increase with time but changes in the shape of the distribution are not typically observed. However, in this study, the shape of the plant height distributions measured in the field did not exhibit a consistent behavior, and changed over time. In general, maize populations remained approximately normal (or at least with zero skewness), while *A. theophrasti* populations became positively skewed or bimodal over time, the former behavior observed predominantly under high competitive pressure from maize in LE, and the later behavior in all other treatments. These results suggest that relative growth rates of the component plants within a species cohort differed especially when the cohort was exposed to high competitive pressures for light.

Among cohorts, there is clear evidence of competition for light, as is illustrated by the lower growth rates and lower final size of the *A. theophrasti* plants in the late emergence treatment (Figure 2.3). This is also evidenced when analyzing the vertical

distribution of the leaf area within the canopy (Figure 2.4). While maize maintained a similar shape and range in the vertical leaf area distribution, the vertical leaf area distribution of *A. theophrasti* was shifted towards the lower layers of the canopy when plants emerged after maize. In contrast, a relatively small advantage is observed for the early emerging *A. theophrasti* considering that early and late emergence are about the same number of days before and after emergence. These results suggest that for a limited range of environmental variation (three years of data) the initial conditions and the initial sizes of the plants were major determinants of the final position within the canopy, shifting the role of the *A. theophrasti* cohort from dominant competitive to dominated and suppressed. Furthermore, none of the three years had comparable competitive outcomes, highlighting the difficulty of predicting competitive interactions among annual plants under variable environmental conditions.

Implications of variable community structure for resource use

The total amount of soil water used over the season by the three contrasting field treatments was not significantly different from each other within each year (174 ± 6.1 , 206 ± 11.0 , 193 ± 7.8 for 2005, 2006 and 2007 respectively). Note that since soil evaporation mainly draws water from the top 0 to 0.05m, we estimate that field measurements did not fully capture soil evaporation, therefore field measured water extraction is considered to be equivalent to water use by the transpiration stream, with the assumption that root soil water uptake in the surface soil layer (0-0.05m) and soil water evaporation below the surface soil layer (0.05m) are small or at least cancel out. What did significantly change across treatments was the partitioning of the water use among the competing species. Using the model, simulations for the conditions of the 2006 experiment were carried out.

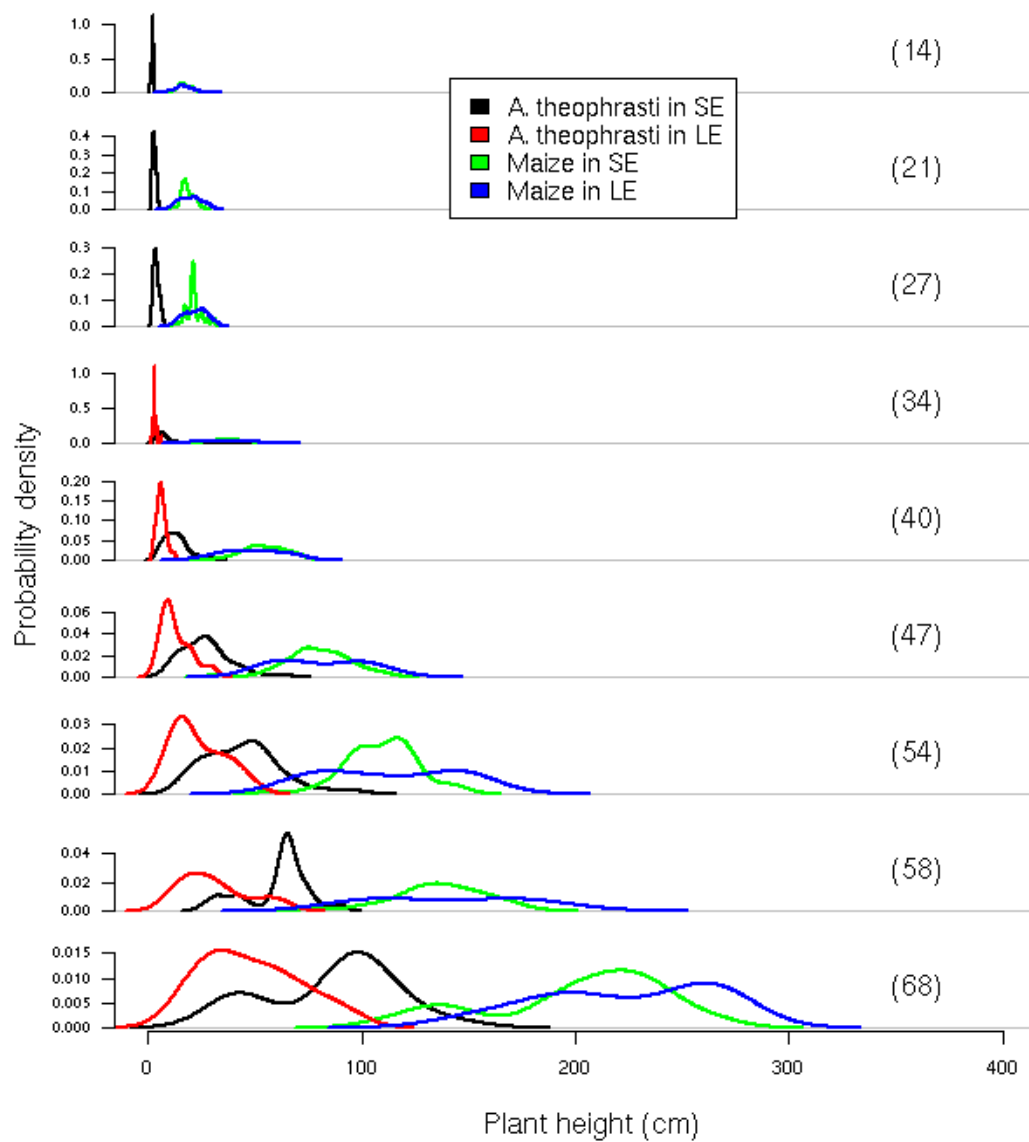


Figure 2.2 Probability density functions of plant height measured in the 2007 field experiments over time. Numbers in parenthesis are days after emergence at which measurements were taken (n=25).

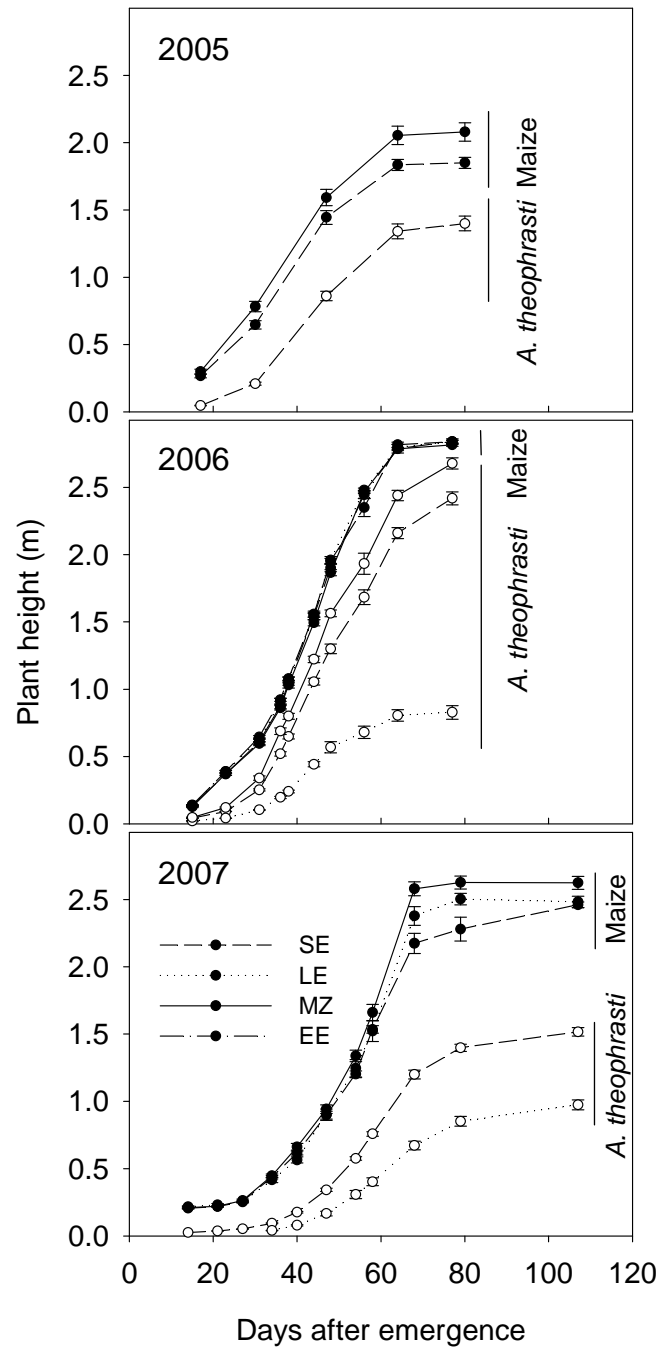


Figure 2.3 Evolution of canopy height in the field for the early, simultaneous and late emergence weed treatments (EE, SE and LE respectively). Open symbols correspond to *A. theophrasti* and closed symbols to maize. Not all treatments are present in all years. Error bars are standard errors of the means (n=25).

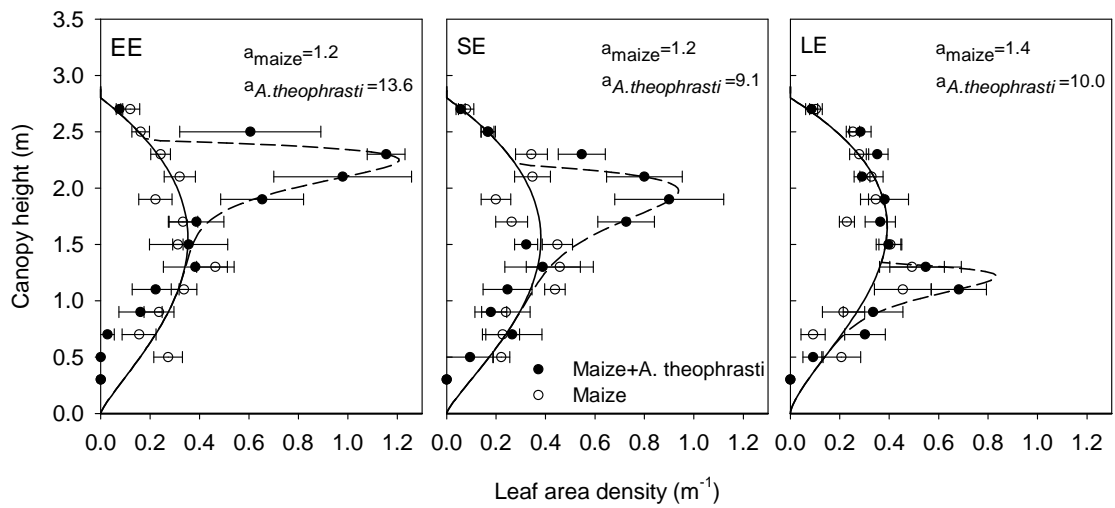


Figure 2.4 Vertical distribution of leaf area at maize anthesis in 2006 (63 DAE), for the early, simultaneous and late emergence weed treatments (EE, SE and LE respectively). Open symbols correspond to maize and filled symbols to maize plus *A. theophrasti*. The dots are field measurement means and standard errors of the means, and the lines are best fit functions using a one parameter equation (Eq. 11). Shape parameter (a) were not statistically different across treatments.

Figure 2.5 shows the time series of soil water use, discriminating among water transpired by maize, *A. theophrasti* or evaporated from the soil surface and the soil water use estimated from the soil moisture measurements in the field, showing a good agreement between total transpired soil water use and field measured soil water use. While the total amount of water used by plants and evaporated from the soil remained approximately unchanged, the shift in species dominating the canopy (*A. theophrasti* in EE and maize in LE) was accompanied by a shift in species cohort water use. This highlights the relevance of the positioning of the canopy elements within the canopy, and the establishments of hierarchies (in this case imposed through planting time) on water use, and biomass production. While early emerging cohorts of *A. theophrasti* were able to intercept a large proportion of the incoming solar radiation from the beginning of the season, allowing them to achieve large growth rates to maintain their status, late emerging cohorts of *A. theophrasti* hardly manage to survive, intercepting a small proportion of the incoming solar radiation and also using a small proportion of the available soil water.

Exploring environmental drivers of community structure

Simulations were conducted to evaluate the effects of resource availability on the intensity and dynamics of competition among plants (Figure 2.6). Three scenarios were simulated, a) one representing the growing conditions (plant density, soils and weather) of 2006 (already presented in Figure 2.5 central panel), b) a shortage of soil nitrogen (fertilization at planting 33 kgN ha⁻¹ instead of 165 kgN ha⁻¹) and c) a drought (precipitation reduced to 1/3 the amount observed in 2006 while maintaining its distribution).

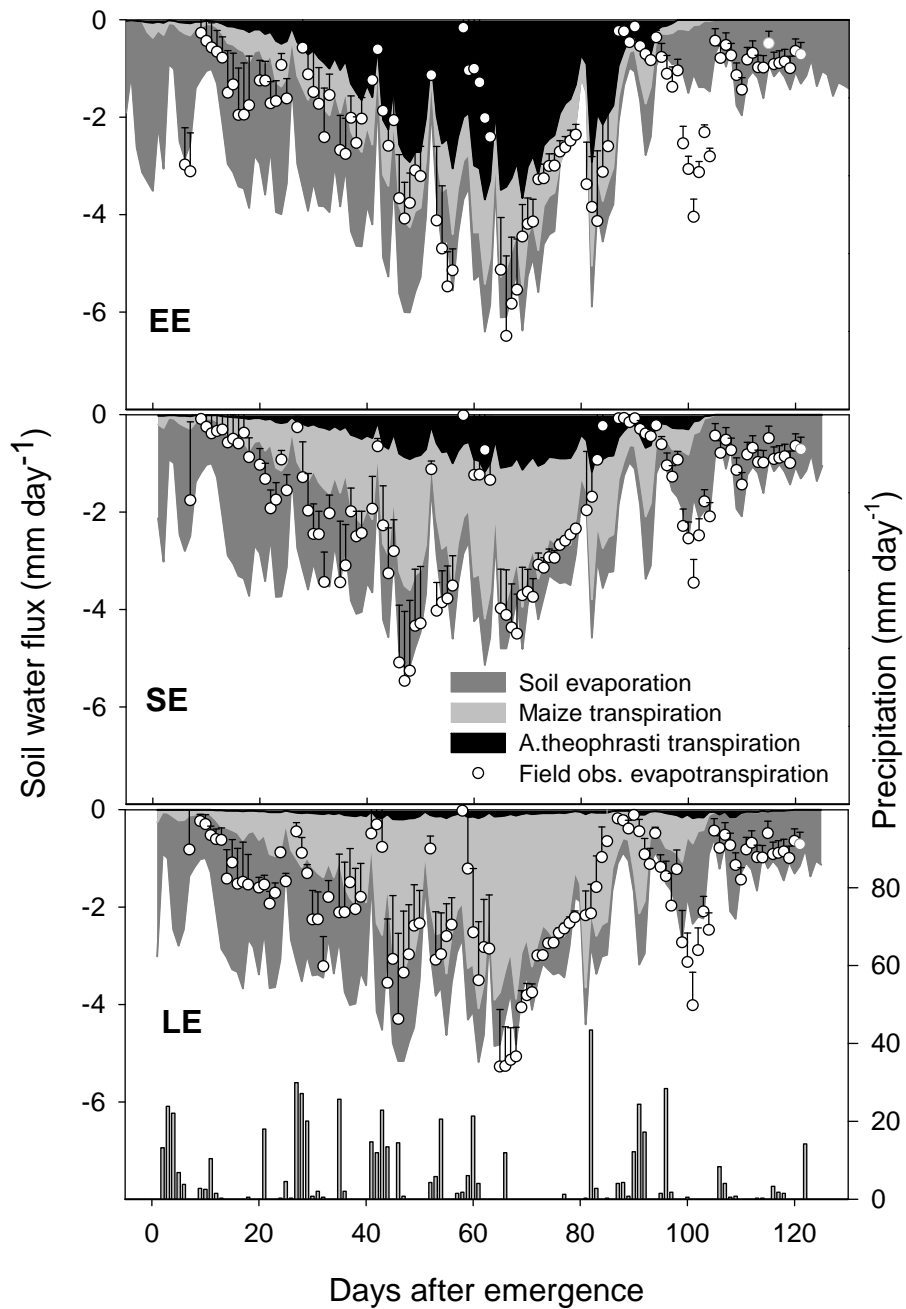


Figure 2.5 Season-long water use during 2006 for the *A. theophrasti* early emergence (EE), simultaneous emergence with maize (SE), and late emergence (LE) treatments as observed in the field (dots are means and bars standard errors of the means, $n=5$) and simulated by the model (shaded areas) .

The initial imposed plant height distributions (10 DAE) for maize and weeds were normal (10% coefficient of variation), and plants started to grow and compete for resources from the beginning of the simulations. However no clear tendency in the formation of size hierarchies evolved until competition for light started to intensify around 60 days after emergence. After this time, the simulations show an increase in plant height skewness over time, with the largest increases observed when growth conditions are favorable, the canopy develops quickly and final leaf area indexes are large (i.e. >4.0). In contrast, lower increase in skewness are observed for scenarios b and c where the canopy grew at smaller rates and reached lower final leaf area indexes (3.4 and 2.9 respectively). Among species, *A. theophrasti* cohorts tended to be more skewed than maize, probably because they were subject to larger competitive pressure for light than maize due to the lower initial stature of the plants. More positively skewed species cohorts are evidence that a small number of plants capture and utilize for growth a relatively large proportion of the resources, growing larger (in size) than the rest of the plants in the cohort.

The changes in resource availability observed in the field experiments and simulated in scenarios *a*, *b*, and *c* impacted the dynamics of competition as well as the structure of the plant community. Resource availability also impacted the total amount of resources used and the partitioning among species cohorts. Drought conditions as simulated in scenario *c* (Figure 2.7) or observed in the field experiments of 2005 (data not shown) reduced the total water use as plants restricted transpiration with simulated reductions from 51% in scenario *a* to 40 % in scenario *c* in the share of transpiration as a percentage of total water use. The largest reductions were observed in the *A. theophrasti* component of the canopy which was 27% of the total canopy transpiration in scenario *a* and only 17% in scenario *c* (Figure 2.7).

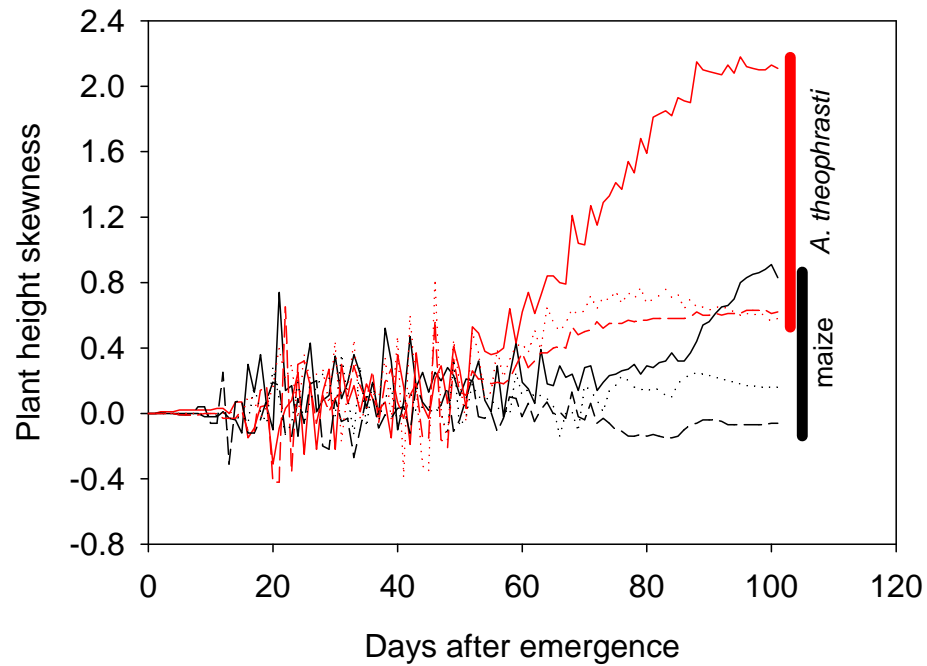


Figure 2.6 Evolution of simulated plant height skewness under three contrasting resource availability scenarios: a) Solid line - conditions of field experiment in 2006; b) dotted line - conditions of field experiment in 2006 but with deficient soil N fertilization of 33 kg N ha⁻¹ at planting; c) dashed line - conditions of field experiment in 2006 but with rainfall reduced by 1/3) (n=90 and n=110 for Maize and *A. theophrasti* respectively).

Reductions of the same magnitude (51% vs. 36% and 27% vs. 17%) were observed when comparing the relatively dry 2005 field season to the 2006 season (scenario *a*). In a similar way limitations in soil nitrogen availability (scenario *b*) reduced total canopy transpiration to 45% of the total water use with the largest reductions being observed in the *A. theophrasti* component that represented 17% of canopy transpiration (Figure 2.7). While *A. theophrasti* did not increase its water use either in absolute terms or in comparison with maize, it did benefit from a less dense and competitive canopy, accumulating slightly more shoot biomass relative to maize in scenarios *b* and *c* (*A. theophrasti* share of total shoot biomass was 6.6, 9.1 and 9.9 % in scenarios *a*, *b* and *c* respectively). Overall, limitations in soil nitrogen availability or soil water availability resulted only in minor advantages for *A. theophrasti* in terms of biomass accumulation, probably due to the lower growth of maize and a less dense canopy that allowed the *A. theophrasti* cohorts to intercept a larger share of the light. It is also interesting that under water stress conditions the relevance of *A. theophrasti* as a sink for soil water decreased, making it even less important in the crop water balance.

Spatial arrangement effects

Spatial arrangement of *A. theophrasti* plants did change the competitive relationships among plants, through changes in the local environment. Increasing proximity of *A. theophrasti* rows to maize rows reduced size inequality and plant height skewness within the *A. theophrasti* cohort (Figure 2.8). This is probably the result of increased competition for light with maize (which always started with larger stature) reducing growth, and in particular reducing growth of the largest *A. theophrasti* plants thereby decreasing their potential to break away from other *A. theophrasti* plants in the cohort.

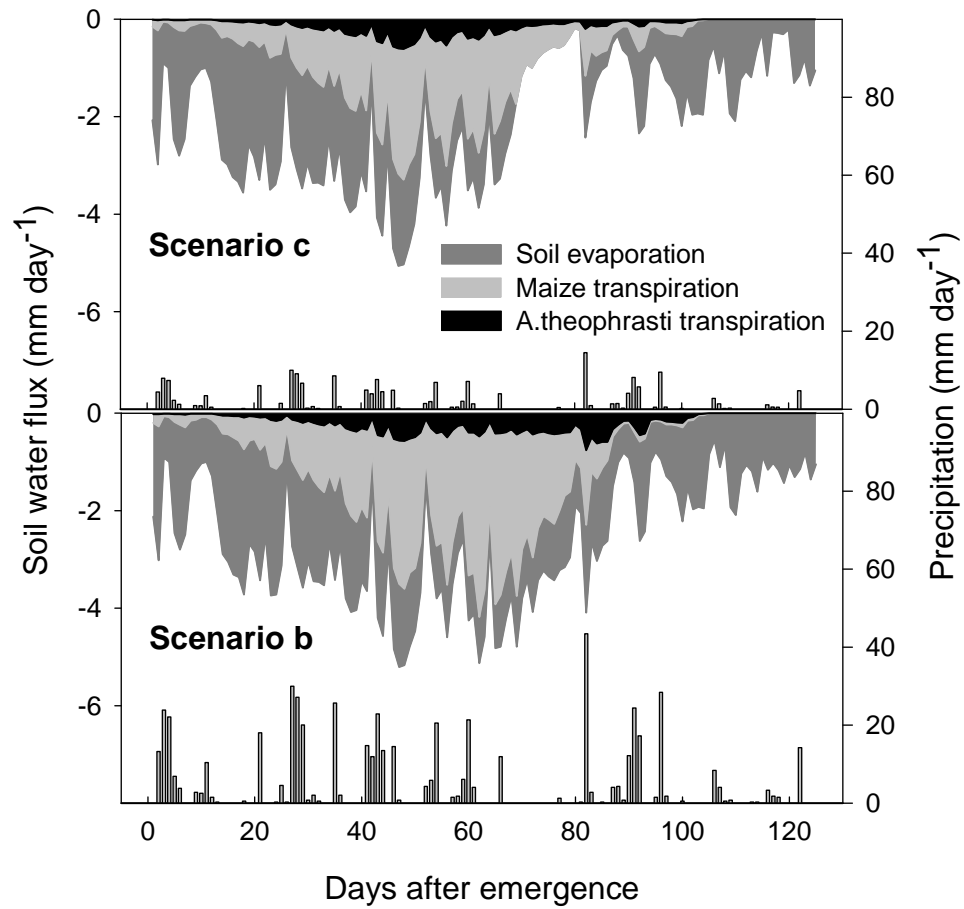


Figure 2.7 Season-long water use during 2006 for the *A. theophrasti* simultaneous emergence with maize (SE) treatment simulated for two contrasting resource availability scenarios. A detailed description of scenarios is presented in the text and Figure 2.6. Simulations are comparable to those in Figure 2.5.

It is not only the intensification of competition for light that leads to height inequality and the positive skew evolution, but also the opportunity of the largest plants to capitalize on their dominant position. For example, if the dominant plants in the cohort are not able to access significantly larger amounts of light than the rest of the cohort because they are shaded by an even taller cohort, they would not be able to break away from the rest of their cohort, but will be able to do so only if general growing conditions are favorable.

Spatial arrangement of *A. theophrasti* plants altered maize growth and yield differently at different plant densities. Figure 2.9 shows results for two contrasting years (2004 and 2007) selected from a series of years for being a low and a medium-high yield loss year. Crop yield loss due to *A. theophrasti* interference increased with decreasing increments with *A. theophrasti* plant density, in agreement with previous works that suggested a rectangular hyperbola function to describe the density-yield loss relationship (Cousens 1985). Increasing proximity of *A. theophrasti* plants to the maize row reduced yield loss in general; however for the scenario with the closest *A. theophrasti* rows yield loss was high even at low densities, suggesting some degree of density independence, especially in 2004 which was a favorable year in terms of early development, subsequent growth and competitiveness for *A. theophrasti*. The random arrangement of *A. theophrasti* plants showed similar behavior as the scenario with rows at 1/3 and 2/3 of the inter-row space, with a tendency to have comparably larger variances in plant height distributions.

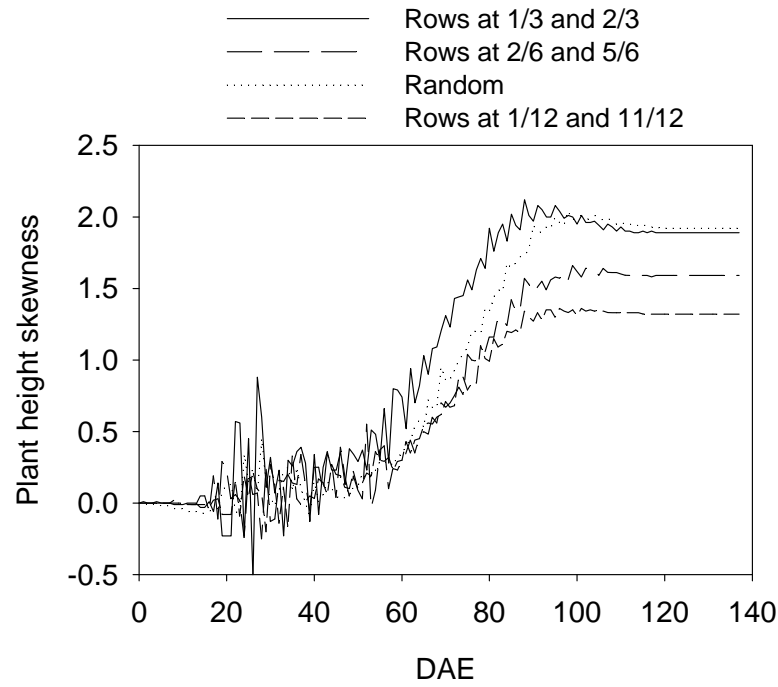


Figure 2.8 Evolution of simulated plant height skewness in 2004 for four maize-*A. theophrasti* mixtures differing in the spatial arrangement of *A. theophrasti* plants. (Fractions in legend are the locations of each of two *A. theophrasti* rows, as a fraction of maize inter-row spacing)

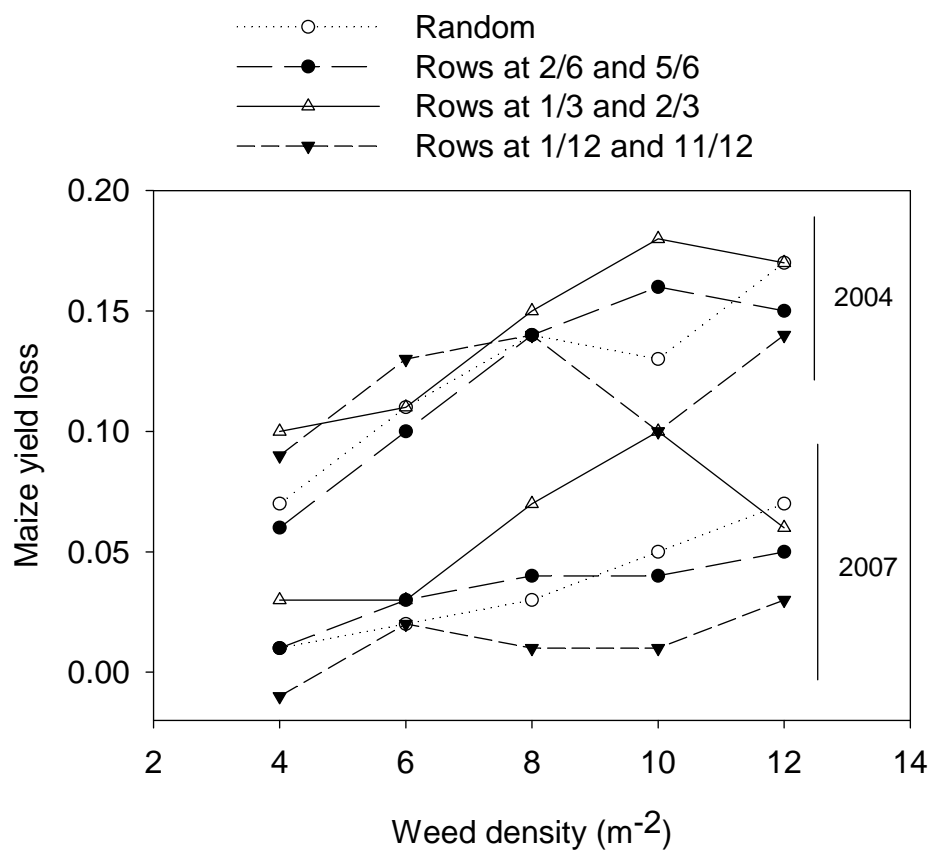


Figure 2.9 Simulated Maize yield loss (1-treatment yield/control yield) in two contrasting yield loss years (2007 low and 2004 high) as a function of A. theophrasti density and plant spatial arrangement. (Fractions in legend are the locations of each of two A. theophrasti rows, as a fraction of maize inter-row spacing)

DISCUSSION

Size hierarchy formation and evolution of plant size distributions

Size inequality has been used as a measure of performance of individuals in a plant community, and ultimately as a measure of the success of that individual in surviving and reproducing (Kokko, Mackenzie et al. 1999). Size hierarchies can be formed as a result of growth and divergence of groups of individuals, or could be established by the initial conditions. In this work, the initial conditions (i.e. establishment time) of the two species cohorts of plants (maize and *A. theophrasti*) played an important role in defining the structure of the canopy and the competitive relationships between cohorts. Early emerging *A. theophrasti* plants formed a dominant hierarchy of plants, while late emerging *A. theophrasti* plants were completely dominated by maize. Within each group and among groups, size inequality increased over time as evidenced by the increases in variance, and divergence of the groups without a clear trend in the evolution of the shape of the distribution for maize and *A. theophrasti* cohorts (Figure 2.2). It was expected based on previous modeling (Yokozawa 1999) and field work (Yokozawa 1999, Vega, Sadras 2003) that crowded species cohorts would become more positively skewed over time as a sign of size asymmetric competition, where large plants preempt light capture and acquire a larger proportion of it in relation to their size (Freckleton, Watkinson 2001). This behavior was only observed in the field for the dominated late emerging *A. theophrasti* cohort in LE treatment, but not in all *A. theophrasti* cohorts; however it was clearly observed for *A. theophrasti* in all model simulations. This suggests that the competitive pressure for light must be high in order for the plant population to evolve positively skewed in

plant height, and to observe increments in skewness as competition intensifies even further. It also suggests that when competition for light is not too intense (i.e. *A. theophrasti* in SE and EE) plants may change their height-biomass allometry (Weiner, Thomas 1992) reducing height at comparable plant biomasses. This point is supported by field observations and by the model results acting as a null hypothesis because the model used a fixed allometric relationship between plant height and shoot biomass. It is also supported by the careful examination of Figure 2.2 which suggests that the negatively skewed (bimodal) distribution of *A. theophrasti* heights developed after 58 DAE, could be the result of a reduction in the rate of height growth of the largest plants in comparison to the plants in the middle of the distribution.

The results from this study are also in agreement with those reported by Vega (2003) for maize, soybeans and sunflower, in that maize did not significantly change skewness over time, while other species, like sunflower and soybean (comparable to *A. theophrasti* in our case) showed significant changes in skewness over time. This is attributed to the planophyle canopy architecture and to the concentration of leaf area at the top of the canopy in all of these other species except for maize, positioning maize as a weak competitor for light when comparing equally sized plants despite its high photosynthetic capacity per unit leaf area (Vega, Sadras 2003). As a result individual maize plants tend to compete less asymmetrically than the individual plants of the mentioned species.

Our simulations suggest that spatial arrangement of the plants is relevant in years where competitive interactions were strong as well as in years where competitive interactions were weak (Figure 2.9), contrasting with previous results obtained with simpler simulations models that suggested that spatial patterns were mostly relevant at low densities and under symmetric competition (Hara, Wyszomirski 1994). The discrepancy may arise because the model used here fully captures the

three-dimensional architecture of plants and it is more likely to obtain better results as it fully describes light interception which is the most important resource involved in size asymmetric competition (Freckleton, Watkinson 2001). Experimental work in agricultural fields in fact suggest important effects of the spatial arrangement at all densities, with decreasing competitiveness of the dominant hierarchy of plants when widening the row spacing (Olsen, Kristensen et al. 2005), in agreement with our simulations.

Resource availability effects on size inequality and canopy hierarchy formation

Reduced resource availability (i.e. soil nitrogen and soil water) resulted in increased competition among plants, increased inequality and increased differentiation of hierarchies within the canopy in agreement with previous work (Fahey, Battles et al. 1998, Anten, Hirose 2001, Nambiar, Sands 1993). Two paths may lead to this result, change in the form of competition (from symmetric to asymmetric), or decreased speed of growth and therefore decreased speed at which competition occurs (Morris, Myerscough 1991). Results suggest both paths as important; under high resource availability increased rates of growth allowed maize to become dominant earlier in the season, and increase size asymmetric competition over *A. theophrasti*. However, under stress conditions, *A. theophrasti* cohorts managed to accumulate relatively more biomass, using relatively fewer resources (soil water), suggesting that it was the alleviation of the competition for light, and not the alleviation of the competition for soil water what allowed such increments in biomass accumulation. In fact competition for soil resources started late in the season, as plants depleted the stocks, and once competition for light has already become intense. Thus it is expected that changes in the light environment and size of the canopy had a large impact on the

dynamics of growth. In a simulation study, Hara (1994) demonstrated that a plant population undergoing strongly asymmetric competition is not so sensitive to fluctuations in environmental conditions which generate variations in physiological parameters (i.e. stable system), whereas a plant population undergoing symmetric competition is highly sensitive to those fluctuations. It seems relevant therefore that competition for resources is dynamic, and changes continuously over time as the winners and losers in the race capitalize on their competitive advantage. Furthermore, it is hard to draw a line separating periods or scenarios of size symmetric vs. size asymmetric competition and even harder when resource availability and resource use itself may change the location of this fuzzy divide. The utility of the concept of size symmetry-asymmetry beyond its descriptive use becomes questionable, as it may be changing continuously and in response to the outcomes of competition. In this context our study agrees with previous works that highlighted the interconnection of above and below-ground competition, and the important role of resource capture preemption (Craine 2005, Craine, Fargione et al. 2005) in a dynamic rather than static race for growth using available resources.

Size inequality and hierarchies formation effects on resource capture and competition among plants

The evolution of size inequality within the canopy, and the eventual formation of hierarchies (in this study triggered by initial differences in plant size) drastically shaped the way resources are captured and partitioned among the components of the canopy. While this observation is not new in the ecological literature (Berntson, Wayne 2000) there are a limited number of studies providing quantitative estimations through field work and modeling. In fact, for agricultural systems such as the one

described in this work, the role of suppressed and dominant plants remains largely unquantified except for a few studies (Faurie, Soussana et al. 1996, Massinga, Currie et al. 2003, Liedgens, Frossard et al. 2004, Berntsen, Hauggard-Nielsen et al. 2004), with the frequent assumption that all plants when present are consuming valuable resources or are modifying their competitors ability to capture valuable resources independent of their position within the canopy and rates of growth (Rajcan, Swanton 2001). This study highlights the dynamic nature of growth and resource capture among competing species, as well as the large sensitivity to initial conditions. These are systems with highly variable outcomes, depending on the time course of environmental conditions, thus making it difficult to develop generalizations about competitive relationships.

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CHAPTER 3

NITROGEN STRESS AND IN SEASON WEATHER EFFECTS ON MAIZE- VELVETLEAF COMPETITION ANALYSED THROUGH AN INDIVIDUAL BASED MODEL

ABSTRACT

Soil nitrogen (N) status and within season weather are important mediators of crop-weeds competition, although the mechanisms for this are somewhat poorly understood. The objective of this study is to explore through a modeling exercise the effects of N and weather on competitive growth of velvetleaf (*Abutilon theophrasti* M.) and maize, considering the year-to-year climatic variability and the interactions that may arise among soil N, soil water, weather and plant growth. For this purpose a mechanistic individual based model was developed, which estimates light interception, photosynthesis, respiration, growth, photosynthate allocation and root growth at the leaf or plant level, allowing plants to compete for solar radiation and soil resources. It also included a detailed model of soil processes, calculating soil organic carbon mineralization, soil temperature, soil water transport, and N losses through denitrification and leaching. Results suggest that maize relative grain yield loss induced by weed competition decreased at higher soil N levels (i.e. on average from 22% at high N to 12% at low N), and in particular decreased more when other environmental factors allowed high maize yield potentials. The effects of soil N and in season weather were also observed in changes in the relative heights of maize and weeds, which were closely related to maize yield loss and therefore a good early

predictor of maize yield loss when maize heights reached 0.6-0.8m. Weather effects on yield loss were guided primarily by changes in soil N availability and in the rates of plant growth that modified both N uptake and the dynamics of competition for other resources. The model results also highlight that maize-*A. theophrasti* competition is highly dynamic, and dependent on the initial conditions, primarily plant sizes and rates of growth.

INTRODUCTION

The effects of nitrogen availability on plant growth have been long recognized; however, it is just recently that its effects on weed-induced yield loss have been considered (Ditomaso 1995, Evans, Knezevic et al. 2003). Most of the work has focused on the effects of nitrogen fertilization rates (Ditomaso 1995, Evans, Knezevic et al. 2003, Cathcart, Swanton 2004, Hellwig, Johnson et al. 2002a, Teyker, Hoelzer et al. 1991, Tollenaar, Aguilera et al. 1997), the effects of timing of nitrogen fertilization (Harbur, Owen 2004b) and the effect of localization of fertilizer applications (Blackshaw, Semach et al. 2002) on weed competition. However, very few studies have focused on the effects of soil nitrogen levels on relative crop and weed growth (Blackshaw, Brandt et al. 2003). Moreover, the approach of most research has been descriptive rather than mechanistic, and in most of the studies it was apparent that there were other factors affecting weed- induced yield loss in addition to soil nitrogen levels. Very few studies (Evans, Knezevic et al. 2003, Harbur, Owen 2004b, Berger, McDonald et al. 2007) document the effects of early-season nitrogen status on either crop or weed plant architecture (height or leaf area) as a determinant of its ability to succeed in a competitive environment and enhance further resource capture in the mid

season stages. For example, nitrogen availability in the early season has been suggested to promote changes in maize-weed height differentials (Berger, McDonald et al. 2007, Harbur, Owen 2004a), light transmittance and maize yield loss (Harbur, Owen 2004a). However, Evans et al. (2003) in a study where the soil nitrogen was varied from very limiting to non-limiting for the growth of maize that was weed free, report no change in maize-weeds height differences and weed-induced yield loss when varying nitrogen levels and attribute maize yield loss to other factors such as root development effects on resource capture and allelopathy.

While the intensity of crop abiotic stress events is largely expected to increase under climate change scenarios (Riha, Wilks et al. 1996, Tebaldi, Hayhoe et al. 2006) there is little information on the effects on biotic stress (McDonald, Riha et al. 2004). This is probably due to the fact that effects on biotic stress are much more complicated to predict due to their mixture of direct and indirect effects. Among biotic stress factors, weeds are the most important (Derr 2004, Bridges 1994) representing billions of dollars annually in direct losses of grain yield and indirect losses from herbicide applications (Gianessi 2003). A first step towards reducing losses is therefore to gain understanding of the effect of the major stress factors influencing crop-weed competitiveness and their interactions. Soil nitrogen, soil water availability and early season temperatures seem to be the most important among them.

Maize yield is severely reduced by the occurrence of water stress during the pollination period (Andrade, Echarte et al. 2002) and this has been the focus of most of the water stress related research on maize yield (Campos, Cooper et al. 2004). However, short periods of stress at other growing stages also have detrimental effects on yields, either directly by reducing grain weight or indirectly by reducing biomass accumulation during the vegetative growth stages (Cakir 2004). It has been suggested that velvetleaf (*A. theophrasti*) induced yield losses in maize are closely related to the

occurrence of water stress periods during the mid season. McDonald et al. (2004) conducted a retrospective analysis of 19 experiments and showed that the presence or absence of water stress from 30-75 days after emergence coupled with differences in early-season temperatures (0-15 days after emergence) explained a significant proportion (60%) of the observed yield loss variability due to velvetleaf competition. They hypothesize that water stress during the vegetative growth of maize has an important influence on height development of both maize and weeds, and thereby may alter the dynamics of competition. An analysis of water use and drought effects on competition (Berger et al., 2009, Chapter 1) suggests that evapotranspiration from plant canopies is almost entirely composed of transpiration after canopy closure (occurring at the mid season for dense planted crops such maize) when most of the radiation is intercepted by plant surfaces and not the soil surface. If the crop canopy overtops the weeds, most of the water is transpired by the crop, leaving a small gap of time through the season in which weeds are capable of competing directly for soil water. Thus in this case, most of the competition caused by weeds is expected to be due to shifts in light interception patterns rather than direct competition for water.

The influence of weather factors and management makes soil water and soil nitrogen status highly dynamic throughout the growing season. Moreover, competition for these resources is also mediated by differences in patterns of plant growth. Hence, it is extremely difficult to conduct field experiments that achieve precise control over resource factors like soil nitrogen and soil water. Furthermore, vertical leaf area distribution, vertical light distribution through the canopy and the partitioning of light interception are also highly dynamic properties of crop-weed competition (Andrade, Calvino et al. 2002, Schwinning, Weiner 1998, Hock, Knezevic et al. 2005) and are important factors for determining crop yield losses (Olesen, Hansen et al. 2004, Seavers, Wright 1999). Very few crop-weed competition models include vertical leaf

area distribution (Olesen, Hansen et al. 2004) and the dynamics of growth of individual plants within the population (Breckling, Middelhoff et al. 2006), thus allowing the development of hierarchies within the canopy, and the ability of some plants to overtop their neighbors exhibiting dominance and suppression. A static representation of the competitive status of weeds and maize, for example based on plant densities (Cousens 1985) is unlikely to accurately represent such a dynamic system. The use of robust dynamic simulation models, based on the very basic principles determining plant growth, seems to be a better alternative, capable of simulating the competitive status of crop and weeds in response to the initial conditions and the dynamics of the competition itself. Nevertheless, broad generalizations are expected to be limited, and the outcomes very much dependent on the initial conditions, the dynamics of growth and within season availability of resources.

The objective of this study is to explore through a modeling exercise the effects of soil nitrogen and weather on competitive growth of velvetleaf and maize, considering the year-to-year climatic variability and the interactions that may arise among soil nitrogen, soil water, weather and plant growth.

METHODS

Model description

The model used is a version of the PNM (Precision Nitrogen Management) model (Sogbedji, van Es et al. 2006) that estimates soil processes within the root zone, including water infiltration and redistribution, temperature, organic matter mineralization, and nitrogen transformations and losses by leaching and denitrification. In this model the soil was divided into 20 layers and all fluxes and processes were estimated on a daily basis. The section of the model that simulates plant growth was modified to allow spatially explicit calculations of solar radiation interception for each individual plant using the algorithms of MAESTRA (Wang, Jarvis 1990). Photosynthesis is estimated hourly with an algorithm similar to the one used in Gecros (Yin XinYou, Laar 2005) which uses the Farquhar-vonCaemmerer model (Yin, Van Oijen et al. 2004, Farquhar, Caemmerer et al. 1980) and couples transpiration to photosynthesis through the stomatal conductance, assuming optimal stomatal conductance behavior (i.e. maximum stomatal conductance is determined by the photosynthesis demand for CO₂, and under water deficit conditions it is reduced to match the soil water supply). Allocation of photosynthate is determined using allometric relationships of the form ($y = a \cdot x^b$) among shoot biomass and total plant biomass, and stem biomass and shoot biomass. Plant height (h) and width (w) are determined using allometric relationships to plant above ground biomass (AGB) ($h = a \cdot AGB^b$), with the simplifying assumption that plant morphological plasticity is negligible (Weiner 2004). The volume of soil exploited by each individual plant, which influences the amount of extractable soil water, is also estimated using

allometric relationships with shoot biomass (Berger, McDonald et al. 2006). This model simulates the dynamic processes of growth and competition for resources (e.g. solar radiation, soil water, soil nitrogen), and produces estimates of water use, biomass accumulation, and grain yield. Individual processes within the model were parameterized with either field data from experiments conducted during the 2007 growing season (i.e. plant architecture and soil properties) or data from the literature (i.e. parameters associated with biomass partitioning, tissue nitrogen partitioning and photosynthetic efficiency).

Scenarios and statistical analysis

Simulations were conducted for a 37 year period from 1970 to 2007, with observed daily weather for Binghamton, NY (42.2° N, 75.9° W) (closest long- term weather station to Ithaca, NY) and a soil with the characteristics of a Williamson silt loam soil (coarse-silty, mixed, active, mesic Typic Fragiudept) where field experiments used to parameterize the model were conducted in 2004, 2005, 2006 and 2007.

High soil nitrogen availability (HN), medium soil nitrogen availability (MN) and low soil nitrogen availability (LN) scenarios were simulated. HN was selected to have non-limiting soil nitrogen availability compared to what are common conditions for commercial maize production (MN). In contrast, LN was selected to represent a scenario of low soil nitrogen availability that might be occasionally encountered in production maize fields. The simulated soil nitrogen treatments were established by base additions of nitrogen as ammonium nitrate 20 days before planting, followed by tillage, as it is common practice in the area. Between this time and planting (May 30), inorganic soil nitrogen gains through organic matter mineralization and losses through

denitrification and leaching occurred, thus soil mineral nitrogen at planting varied slightly among years reflecting early weather conditions (347 ± 1.5 , 198 ± 1.4 , 90 ± 0.2 kg N ha⁻¹ in the 0-1m soil profile for HN, MN and LN respectively).

In the simulations, maize plants were arranged in rows 0.75m apart at a density of 8 plants m⁻² and weeds were arranged in two rows located in between maize rows 0.25m from the maize row. Weeds were established at a density of 8 plants m⁻² and emerged at the same time maize plants emerged on May 30. These establishment conditions were similar to the ones used in the field experiments, from where data to calibrate the model was extracted. The initial leaf area of the plants was set to follow a normal distribution with 10% coefficient of variation and mean 100cm² and 10cm² for maize and velvetleaf respectively when plants had 100 growing degree days calculated with a base temperature of 8 °C. Under this individual based model, plants grow independently from each other, all calculations of photosynthesis, respiration, allocation and capture of resources (including light) are made at the plant or leaf level, and plants interact when they acquire resources from the common pool (i.e. soil or solar radiation).

The simulations covered a wide range of soil nitrogen availability scenarios, and all the observed variability in climate that occurred during the 37 year period. The resulting time series of maize yields, and maize grain yield loss (RYL, 1-treatment yield/control yield) were analyzed and compared. Principal component analysis was used to summarize the major external drivers of growth and competition for resources, which were, weather (temperatures and solar radiation), soil nitrogen availability and soil water availability. Each of the resulting principal components (scores) were later regressed against maize yield loss in search for significant relationships.

RESULTS

Interannual variability in maize yield and maize yield losses

Simulated maize yields varied significantly among years due to variations in climate (i.e. temperature, precipitation and solar radiation) (Figure 3.1). In the HN scenario, yields varied within the 4000 to 11000 kg ha⁻¹ range, while scenarios lacking sufficient soil nitrogen showed smaller ranges and lower average yields. These values are consistent with the range of maize yields achieved in New York on similar soils. As shown in Figure 3.1, reductions in soil nitrogen availability increased the chances of higher relative yield losses in most years. The mean and standard error of the yield losses were 0.12 ± 0.009 , 0.15 ± 0.009 , and 0.22 ± 0.01 for the HN, MN and LN scenarios, respectively, indicating increases in maize yield losses as soil nitrogen becomes limiting. Further analysis of the data (Figure 3.2) suggests that the difference in yield loss between HN and LN or HN and MN was larger as the weed-free maize yield of LN and MN increased respectively. This result highlights the interconnection between yield loss, soil nitrogen availability and other environmental factors affecting plant growth and yield. It also indicates that in years where the maize yield potential is high, maize would capitalize on this potential and out compete *A. theophrasti* if enough soil nitrogen is available.

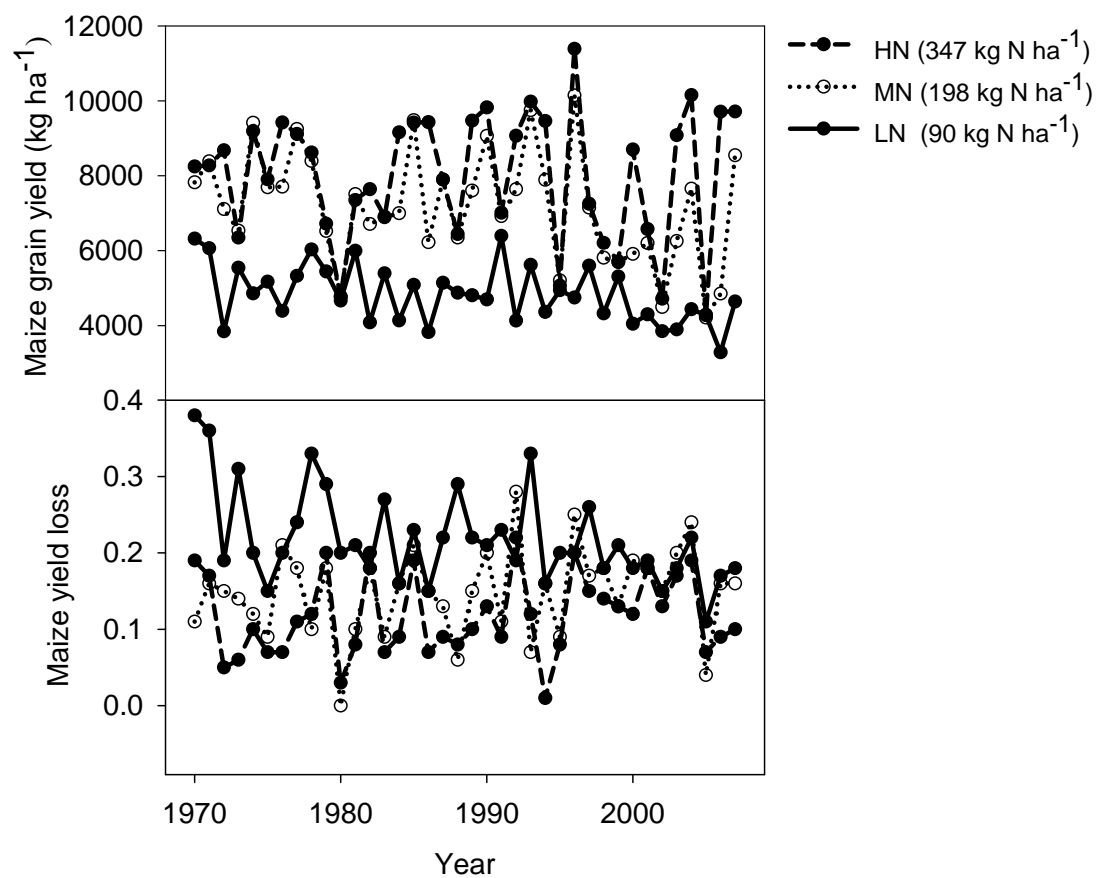


Figure 3.1 Interannual variability of maize grain yield (weed-free) and weed-induced yield losses at three soil nitrogen levels.

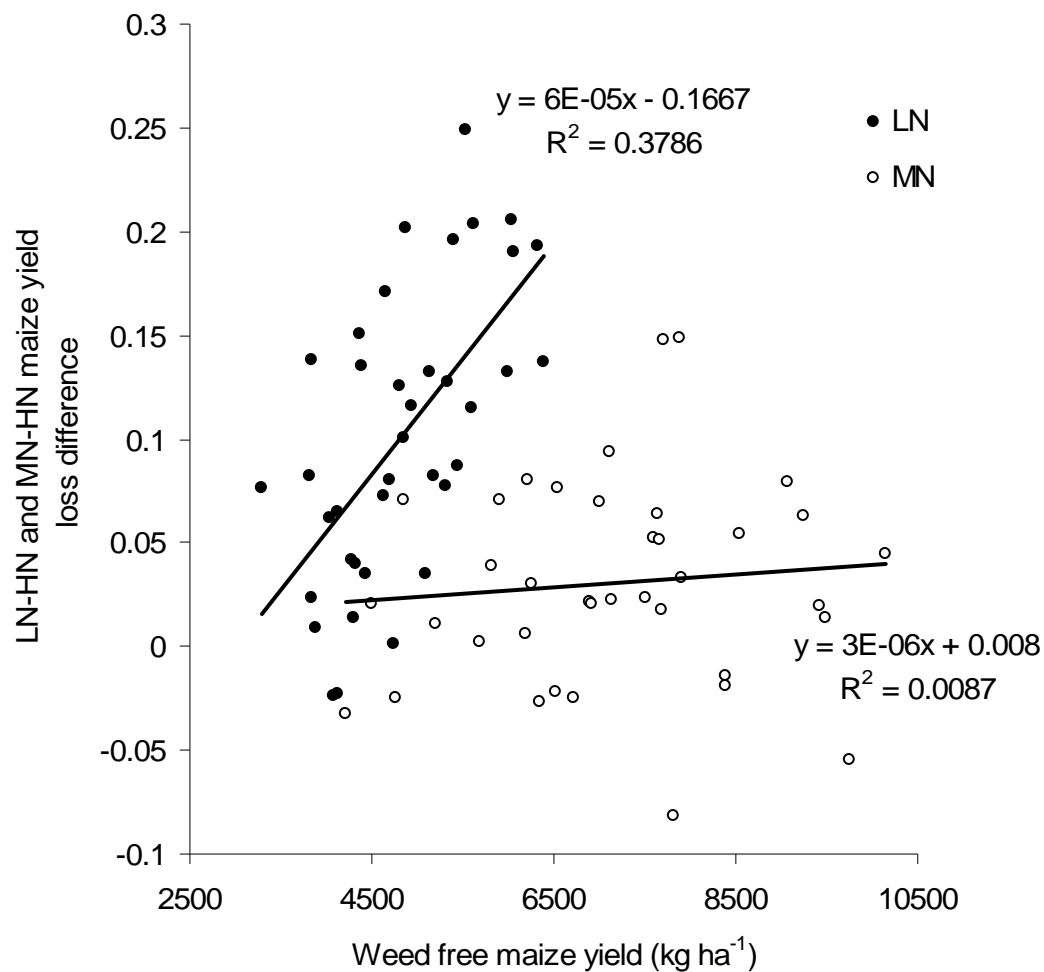


Figure 3.2 Reduction in maize yield loss upon increments in soil nitrogen availability as a function of weed free maize yield loss under low (MN or LN) soil nitrogen availability.

Evolution of canopy heights and determinants of maize yield loss

Canopy heights (i.e. average cohort height) were analyzed to evaluate the dynamics of growth and competition, as well as to identify early predictors of potential maize yield loss and weed competitiveness. Figure 3.3 shows evolution of the difference in canopy height between maize and *A. theophrasti* at different maize heights, thus allowing the comparison of the height differences across treatments in a standardized form with respect to maize. Height differences increase at decreasing increments in most cases, and curves for high and low yield loss scenarios tend to increasingly diverge after maize reaches 0.6-0.8 m height. This height range roughly coincides with the period when most of the solar radiation is intercepted by the combined canopy (>80%) and competition for light intensifies. Canopy hierarchies seem to be set early on, and maintained over time, which is clearly seen when observing that the lines in Figure 3.3 do not cross in general. Also, when the differences in height are larger, maize yield loss is smaller (as indicated by color bar), suggesting that changes in relative canopy height have a large impact on weed interference and maize yield loss. A clearer picture is observed when looking at height differences at anthesis, which is the time where height growth stops (maize) or slows down (*A. theophrasti*) (right side scatter plot). Larger differences in height are associated with higher maize canopies, and are better associated with maize yield loss than the height of maize alone. There is significant variability along the y-axis, most likely due to the influence of other environmental factors such as air temperature, solar radiation and phenology. Lower maize heights imply a sparser canopy and a reduced probability of weed suppression through pre-emptive light interception. Phenology is relevant because the change from vegetative to reproductive growth marks a stop in height growth, thus plant heights will depend on the speed at which plants develop

(relative growth rate) which is generally reduced under soil nitrogen, temperature or soil water stress.

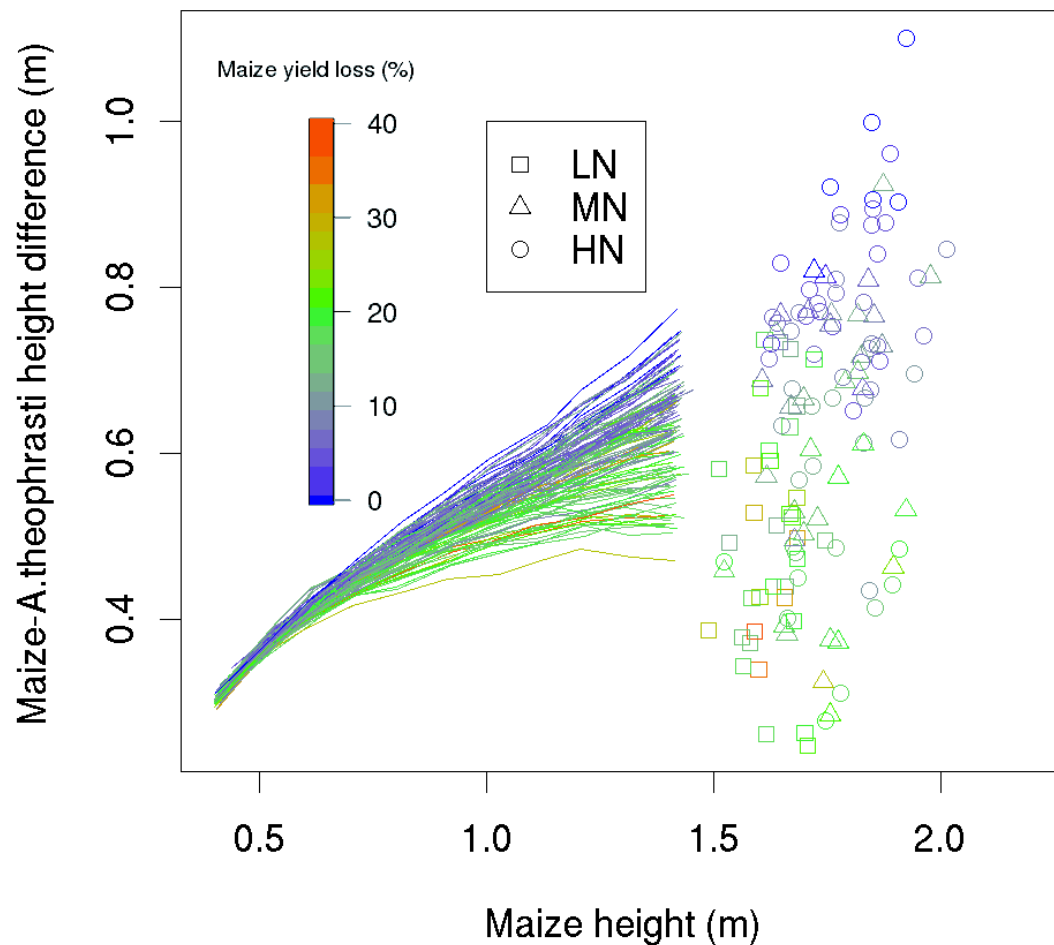


Figure 3.3 Maize-weed height differentials as a function of maize height through the growing season (lines) and at maize anthesis (dots) for different years and soil nitrogen treatments. Line and dot colors correspond to yield loss level as indicated by color bar (n=138). HN, MN, LN stand for high, medium and low soil nitrogen availability.

Principal component analysis was used to decompose selected environmental factors affecting maize-*A.theophrasti* competitiveness into uncorrelated linear combinations of these factors (Table 3.1). Of all seven components, three showed significant correlation with maize yield loss. Those were: PC1, associated with wet, cold and cloudy weather, which was positively correlated with maize yield loss (0.22); PC3, associated with soil nitrogen availability, which was negatively correlated with maize yield loss (-0.63); and PC4, associated with wet, warm, cloudy weather, which was negatively correlated with maize yield loss (-0.32). Together they accounted for 59% of the total variability on the environmental variables analyzed. This results suggests that soil nitrogen was a major driver of the competitive relationships, because wet weather (PC1 and PC4) in the model is mechanistically associated with high losses of soil nitrogen through leaching and denitrification, thus it seems that directly (PC3) and indirectly (PC1 and PC4), soil nitrogen mediated much of the maize-*A. theophrasti* interference. Other factors not included in the model may also be influencing the competitive relationships in the field, and these results have to be taken as a detailed analysis of the model responses rather than a guide to field recommendations.

Table 3.1 Principal component analysis of the major meteorological variables (avgTemp, air temperature at 2m height; solar, PAR solar radiation), soil nitrogen at planting (planting_N), soil water expressed as fraction of transpirable soil water (ftsw), and correlations between principal components and maize yield loss. Variables were averaged in 40day periods (0-40d and 0-80d).

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5	Comp.6	Comp.7
Loadings (eigenvectors)							
ftsw 0-40d	0.16	0.67	0.00	0.25	0.58	0.17	0.33
ftsw 40-80d	0.51	-0.26	0.00	0.32	0.22	0.44	-0.58
planting_N	0.00	0.00	1.00	0.00	0.00	0.00	0.00
solar 0-40d	-0.30	-0.51	0.00	-0.37	0.63	0.26	0.20
solar 40-80d	-0.52	0.35	0.00	-0.12	0.25	-0.16	-0.71
avgTemp 0-40d	-0.34	-0.31	0.00	0.80	0.16	-0.33	0.00
avgTemp 40-80d	-0.48	0.11	0.00	0.21	-0.36	0.76	0.00
Proportion of variance	0.34	0.21	0.14	0.11	0.09	0.08	0.03
Cumulative variance	0.34	0.55	0.69	0.80	0.89	0.97	1.00
Correlations with maize yield loss	0.22	-0.02	-0.63	-0.32	-0.05	-0.17	-0.03
P values	0.01	0.77	<0.0001	0.0001	0.57	0.05	0.77

DISCUSSION

Soil nitrogen effects on maize weed-competitiveness

Under the range of conditions we assessed, soil nitrogen was the largest factor affecting maize and weed competitiveness. Effects were observed as a direct response to the different soil nitrogen availability scenarios (LN, MN, HN) (Figure 3.3 and Table 3.1) or indirectly through losses and gains of soil nitrogen as influenced by temperature and soil water balance.

In previous work (Berger, McDonald et al. 2007) that used the analysis of growth curves, we have shown that the pattern observed in Figure 3.3 can be described in terms of changes in the RGR ratio of weeds and maize, as well as the ratio of the height scaling factor (b in the biomass-height allometric equation) between weeds and maize. The model used in this work is much more detailed and changes in RGR result from changes in leaf level photosynthesis, but a fixed b is assumed for simplicity. Soil nitrogen differentially affected the RGR of weeds and maize, with lower levels of soil nitrogen availability yielding relatively higher RGR for weeds than for maize in the simulations. That could be the result of the direct effect on growth (larger increase in RGR for similar increases in soil nitrogen) or could be the result of changes in light availability due to reduced growth of the maize canopy. This latter effect seems to be extremely relevant, especially when considering the effects of other stressing factors that reduce the overall development of the canopy. A less developed canopy (low leaf area index) offers more opportunities for low stature plants to achieve high RGR because they are allowed to receive a larger share of the incoming solar radiation. Therefore the effects of soil nitrogen availability have to be considered not only in

terms of the direct effect on growth but also on the overall reduction in the size of the mixed canopy. Dense weed infestations can sequester a large proportion of the total soil nitrogen stock early in the growing season, thereby undermining the development of the maize canopy, and bringing more opportunities for weeds to achieve larger RGR and produce larger yield losses. This could particularly be the case in weed communities dominated by grasses that tend to grow at large densities and consume large quantities of soil nitrogen (Cathcart, Swanton 2004, Hellwig, Johnson et al. 2002b). This effect is noticeable in some years in the simulations conducted in this work, even when the weed densities used here were comparably smaller.

Weather influences on maize-weed competitiveness

Weather effects on yield loss were guided primarily by a) changes on soil nitrogen availability (PC1 and PC4 on Table 3.1), with wet years having greater losses and less available soil nitrogen, and b) changes in the rates of growth, with cold years (PC1) (lower development rates) associated with high yield loss and warm years (higher development rates) associated with low yield loss (PC4). There have been very few studies looking at the effect of climate on maize-weed competitiveness (McDonald, Riha et al. 2004) and much more effort is needed to understand the very complex interactions between weather and the growth factors governing maize-weed competitiveness. McDonald et al, (2004) after a country wide analysis of results obtained at field experiments, suggested that mid-season drought (31-75 days after planting) was the main determinant of increased weed competitiveness. They analyzed experiments where nitrogen fertilization was optimal, and therefore the effect of weather on soil nitrogen availability that we observe in our simulations may not have

been expressed as there were no situations where soil nitrogen was limiting plant growth.

Competition, formation of canopy hierarchies and maize yield loss predictability

This study has shown that maize yield loss is highly dependent on initial conditions defined early during the season as evidenced in figure 3, where height difference at 0.6-0.8 m maize height is well related to maize yield loss, suggesting that in particular the relative heights of maize and weeds are good indicators of maize yield loss. This finding agrees with previous studies that have identified different metrics such as height, leaf area cover and above ground plant volume as important determinants of the competitive ability of weeds and crops (Olesen, Hansen et al. 2004, Rohrig, Stutzel 2001, Roush, Radosevich 1985, Bussler, Maxwell et al. 1995). The model described in this paper aims at representing light capture in great detail, together with a reduced set of canopy properties. It does not account for plant plasticity (Weiner 2004) nor does it account for the effects of light quality on plant morphology and growth (Rajcan, Swanton 2001). However, the model is able to capture a large proportion of the expected behavior of weed induced maize yield loss, suggesting that these missing factors are of minor importance. The large sensitivity to initial conditions is likely the result of nonlinearity between plant size, resource capture and plant growth, thus when competition intensifies the initial small differences grow disproportionately. The end result of this process is referred as size asymmetric competition (Freckleton, Watkinson 2001). Once this process has started, the outcomes are highly predictable, suggesting that there could be early indicators of competitive outcomes. In our analysis, we used the average height of plants and its difference, which seems likely to differentiate, at least, low (e.g. <10%) vs. high (e.g.

>10%) maize yield losses once maize plants have reached 0.6-0.8m height.

In the current study simulations are conducted independently for each year; seed production, seed bank size and stover production were not considered. This approach was selected as our focus was on understanding changes in competitiveness of standardized crop-weed stand. In the real world, yearly outcomes of competition will be carried on from one year to the following year through seed production. Therefore, weed density will also contribute to the year to year variability in yield loss. The combination of large variability induced by environmental factors, and the nonlinearity in the plant size-seed production relationship (larger plants produce disproportionately larger amounts of seed) may result in chaotic behavior of the time series (Sakai 2001). This would make long term predictions a challenging problem, and suggests that early season assessments of the competitive status of weeds may be a better option than long term predictions of weed competitiveness.

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